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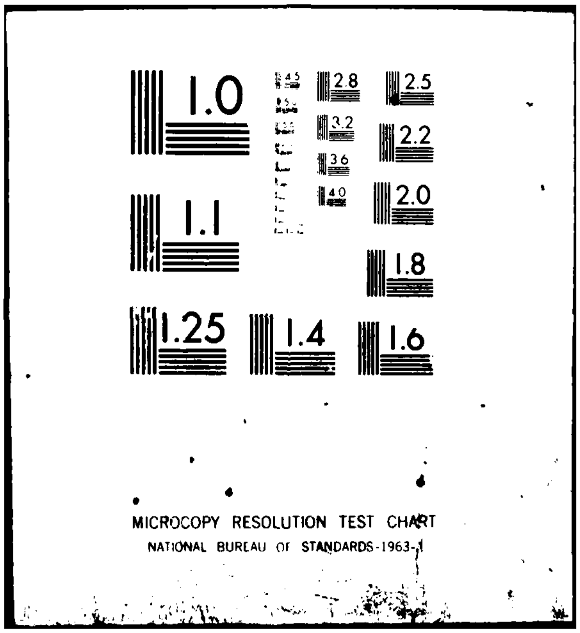
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The population ecology of a rare and endangered plant species, 'Cirsium rhothophilum' on Vandenberg AFB, California

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Final Report, 15 May 78 -

for the

Air Force Office of Scientific Research

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1.0 Preface

The opinions expressed in this report are those of the authors and do not necessarily represent the views of the U. S. Air Force or any of their employees. The authors will appreciate being informed of any errors or omissions.

2.0 INTRODUCTION

On military installations like Vandenberg AFB it is possible to combine the conservation of valuable natural ecosystems with the national defense mission. The base operations emphasize high technology and require relatively small numbers of support personnel concentrated in restricted and mostly permanent locations. Large areas of the base are little disturbed from their natural condition, and many areas formerly disturbed have actually reverted to natural vegetation under Air Force management. With care, it should be possible both to meet the goals of the Air Force and to insure the continued existence of plant and animal species in this unique and interesting part of coastal California.

This is a report of a study carried out on Vandenberg AFB and directed primarily towards one species--the Surf thistle (*Cirsium rhothophilum*)--a rare plant restricted to the coastal dunes of Santa Barbara and southern San Luis Obispo Counties. The study was undertaken in the belief that this species can be protected without having to impose unrealistically severe restrictions on the operation of the base. But even though the scope of this study is narrow, we hope that it will have implications for the entire dune ecosystem, for all of Vandenberg AFB, and perhaps for other Air Force installations faced with problems in the management of rare and endangered species.

The practical problem addressed was this: What is the status of *Cirsium rhothophilum* a proposed rare and endangered species, and how are present and future base activities likely to affect the welfare of this plant? Even from this very short-range and limited point of view, the question is of importance to the Air Force. Federal and state agencies will almost certainly require at various times in the future that the impact of development and management practices on *Cirsium rhothophilum* and other species of the dunes be evaluated. To do this to the satisfaction of the technical staff of these agencies, detailed information will be needed. From a longer range and broader point of view, the study was designed to improve our understanding of the ecological relationships of the Vandenberg dune plants in order to suggest how the dunes might be managed and to provide baseline data against which to compare future conditions of the dunes.

Even the most limited of the stated goals is difficult to achieve in a single year's study. Dune ecosystems are dynamic, and it is unlikely that the conditions in any two years will be the same. Only with long-term studies that include a substantial sample of the year-to-year variability can statements about change in ecosystems be made with confidence. The conclusions reached in this study are made on the basis of limited data, and may well have to be revised as more and better data accumulate.

3.0 ORGANIZATION OF THE REPORT

The organization of this report is based on the recognition that some readers will be primarily interested in the major results and conclusions of the study, while others will want to examine the scientific data carefully. The report therefore separates the more esoteric science from the application. The major results and recommendations are given after a brief section outlining the study in general terms. The scientific data on which the conclusions are based are given in two appendices. To facilitate possible later publications, these have been written as self-contained documents, and they may therefore repeat some of the information given in earlier sections. Appendix A reports the results of the dune survey, and Appendix B the results of the *Cirsium rhothophilum* population study.

4.0 SCOPE AND DESIGN OF THE STUDY

The work reported here was restricted to the active dune areas of Vandenberg AFB, and emphasized *Cirsium rhothophilum*. Since this species occurs only in the area of moving dunes, all of the permanent transects and most of the other sampling was confined to this narrow coastal strip, from a few kilometers north of Honda Canyon in south Vandenberg to just above Shuman Creek in north Vandenberg. (See Appendix A).

The study began in late May 1978 and field work was completed in July 1979. Most of the data were collected in three main sampling periods: July through August 1978, January 1979, and July 1979. Permanently marked transects were established at two sites, one in north Vandenberg and one in south Vandenberg. A broad survey was also made that covered essentially all of the active dunes. The general location of the survey transects are mapped in Appendix A, and of the permanent transects in Appendix B.

Data collected in the permanent plots permitted the growth, survival, and seed production in *Cirsium rhothophilum* to be determined. Additional data on plant cover of all species characterized the community in which the transects were located. The broad survey recorded the presence of all species in the moving dunes and the adjacent stabilized areas, and estimated the abundance of _Cirsium rhothophilum_. More complete descriptions of the data collected and the scientific results obtained are given in Appendices A and B. Literature cited will be found in Appendix B.

5.0 PROJECT PERSONNEL AND ACKNOWLEDGEMENTS

This project was the combined work of several persons. Paul Zedler, Professor of Biology at SDSU designed and directed the study and wrote most of the report. Kathleen Guehlstorff, formerly a graduate student at SDSU, helped to design the study, did the bulk of the field work from May 1978 to January 1979, and summarized and analyzed the data collected to that point. Carla Scheidlinger and Clay Gautier, graduate students at SDSU, assisted in the fieldwork in January 1979 and resampled the plots in July 1979. Ms. Scheidlinger had the major responsibility for data processing and is the primary author of Appendix A. Mr. Gautier carried out the germination experiments and wrote the corresponding section of Appendix B. Pam Salish provided valuable assistance in field and laboratory work.

We wish to acknowledge the assistance of Jim Johnston and Allan Naydol of Vandenberg AFB, and Major Al Young of OEHL, Brooks AFB, in carrying out the project on Vandenberg AFB. Dr. W. Berry of AFOSR and Major R. C. Wooten of SAMSOE provided assistance and encouragement in the planning phases of the work.

6.0 SUMMARY OF MAJOR RESULTS

6.1 Legal Status of _Cirsium rhothophilum_.

As of 10 November 1979, _C. rhothophilum_ is not among the species given special protection under either the U. S. Rare and Endangered Species Act of 1973 or the Native Plant Protection Act of the State of California. However, its endangered status has been recognized and recorded by the Federal Government (Greenwalt 1976) and by the California Native Plant Society (Powell 1974). It is very likely that _C. rhothophilum_ will eventually achieve formal status as endangered.

According to Mr. Joe Dowhan of the Office of Endangered Species, U. S. Fish and Wildlife Service; C. rhothophilum is a "candidate species" scheduled for detailed evaluation. It will probably be listed eventually but since it is not thought to be in immediate peril, it is not among those species being proposed in the next year. However, there are special "emergency rule making" procedures which allow the almost immediate listing of species facing imminent danger. Unless there is a major change in the management or utilization of the dunes, it is unlikely that these emergency procedures would be applied to Cirsium rhothophilum.

Eventual listing of C. rhothophilum by the State of California is also very likely. Mr. Stephen Rae of the Endangered Plant Program in the California Fish and Game Department stated that C. rhothophilum is being "actively considered" for legal recognition, with an excellent chance of eventual recognition. If it were to be listed, it is unclear that the State would have jurisdiction on Vandenberg AFB. Most likely some cooperative arrangement between state and federal agencies would be sought.

The work reported here is the first detailed population study of C. rhothophilum, and will probably be evaluated by both the California Fish and Game Department and the U. S. Fish and Wildlife Service. Informal discussions suggest that in the balance our findings will support listing. However, since we report a relatively large and well-distributed population, this study also reinforces the view that C. rhothophilum is in no immediate danger of extinction. C. rhothophilum will probably not have the highest priority for listing unless major changes in land use are made.

6.2 Population size and distribution on Vandenberg AFB

The broad dune survey conducted in January 1979 and reported on in Appendix A showed Cirsium rhothophilum to be widely distributed but highly clumped. It occurred in only nine out of 766 m^2 plots placed over the entire dune area, a frequency of only one percent. But the scattered populations can contain a large number of individuals, and estimates of numbers of plants gives an average density for the entire dune system of about 120 plants per hectare (48.6 plants per acre). Since the total area of the dune is estimated at more than 668 hectares (1650 acres) (Coulombe and Cooper 1976) the total population is in excess of 80,000 plants. This number seems astronomical, but since annual mortality is estimated at more than 40 percent, it is clear that sheer numbers alone are not necessarily insurance against extinction. Nor are the numbers large when compared to other rare species. For example, Pogogyne abramsii, one of the first species in California to be listed by the U. S. Fish and Wildlife Service, probably has at the end of the growing season an absolute minimum of 175,000 plants within protected areas, and a total population probably ten times this size. Population size can be interpreted only if something is known of the population ecology of the species in question.

C. rhothophilum is found in both the Purisima Point dunes in north Vandenberg AFB, and in the area around Surf near the mouth of the Santa Ynez River south to a few kilometers north of Honda Canyon where the dunes end. Because the available habitat in south Vandenberg AFB is limited, the great majority of individuals are found in the much more extensive dunes in north Vandenberg. C. rhothophilum occurs only in the strip of coast between the beach and the stabilized dunes. It is intolerant of the extreme conditions of the beach and windward slopes of the first dunes, and is also evidently unable to tolerate conditions in the more heavily vegetated stabilized areas. It is a specialized plant, and this presumably accounts for its rarity.

A more detailed account of population size and distribution will be found in Appendix A.

6.3 Population Ecology

The population studies show that Cirsium rhothophilum, like many other Cirsium species is a short lived perennial that usually flowers only once and then dies. New individuals are primarily established from seed, and vegetative reproduction plays only a minor role. In these traits C. rhothophilum contrasts with the majority of the species with which it is found which are longer lived perennials with vigorous vegetative reproduction.

C. rhothophilum plants mostly flower from late spring to mid-summer, shed their seeds in summer and fall and establish new seedlings during the period of winter and spring rains. The populations of C. rhothophilum in the sample plots declined only by 5 percent from July 1978 to July 1979, though about 40 percent of the plants sampled in July 1978 were dead by July 1979.

Rosette growth is highly variable. Many rosettes showed negative growth while others may have doubled in diameter. Part of the variability is due to the feeding of insects which can change rosette dimensions, but the major variation is caused by rosettes being buried by moving sand. Many individuals branch below the surface of the sand. The branching may be another symptom of burial or insect attack, or both.

A growth curve calculated from the data suggests that many of the largest rosettes may be as much as 8 or 9 years old. This is probably an overestimate, but it is certain that most flowering rosettes are probably more than two years old before they flower.

Overall the analysis suggests a dynamic population with many plants dying and becoming established each year. Population size probably fluctuates somewhat from year to year, but the plants live long enough to average out major variations.

A more detailed account of the population ecology of *C. rothophilum* will be found in Appendix B.

6.4 Threats to the population

Cirsium rhothophilum appears to be doing well on Vandenberg AFB. There is no way of knowing for certain if populations are higher or lower than they were 50 years ago, but it is reasonable to suppose that they are not greatly different. Mortality of plants in the year of the study was due to causes that have probably always been operative--physical stress, sand burial, insect attack. The artichoke plume moth causes extensive damage to seeds and leaves, but this most likely has always been the case. Little evidence of destruction of plants by foot or vehicular traffic was seen. Vehicles such as dune buggies could cause a great deal of harm if they were permitted on the dunes. The major threat to *Cirsium rhothophilum* at present is probably the spread of introduced European beach grass, which seems capable of excluding it.

7.0 RECOMMENDATIONS

7.1 Treat *Cirsium rhothophilum* as though it already had legal status.

Cirsium rhothophilum does not have formal legal status as a rare and endangered species at this time. However, it seems inevitable that it will eventually be listed by both the State of California and the federal government. Under the circumstances it would be prudent and responsible for the Air Force to treat the species as though it were already listed. This amounts simply to recommending continuation of the existing policy of cooperation with state and federal agencies to insure the survival of valuable biological resources. As discussed in the following section the preservation of C. rhothophilum should be viewed as the long-term preservation of the entire dune ecosystem.

7.2 Ecosystem based management

This study focussed on Cirsium rhothophilum, but it must be strongly emphasized that we do not advocate single species management. The results of this study suggest that the preservation of the intact dune ecosystem will insure the survival of C. rhothophilum. In the short run the preservation of the dunes should require little more than restricting the encroachment of roads and buildings and limiting access to an acceptable level. Since active dunes depend on sand supply, long term preservation of the dunes may require that the effects of coastal construction and the damming of rivers be considered. Changes in ground water and river flow could also produce at least local changes. Exotic species pose a special problem, discussed in the next section.

7.3 Stop the use of exotic species for erosion control

A number of introduced species are well established in the stabilized and moving dunes of Vandenberg AFB. Some of these species are aggressive and have the potential to exclude native species. European beach grass, (Ammophila arenaria) and Veldt grass (Ehrharta calycina), two species which have been planted for erosion control, could pose a serious threat to the natural vegetation. The European beach grass is most likely to interact with C. rhothophilum, since it has been planted and is thriving in the active dunes. The survey of the dunes showed that few native species generally and virtually no C. rhothophilum grew within dense population of this species. It is reasonable to suppose that the area of C. rhothophilum habitat will decrease if European beach grass increases. Perhaps of equal or greater importance is the change in dune building that may result. C. rhothophilum is most abundant in microhabitats which are actively accumulating sand. If the European beach grass becomes well established on the foredunes, it may produce a nearly continuous high dune which could trap sand and slow its movement inland, starving the landward dunes and possibly reducing the optimal C. rhothophilum habitat. A negative interaction between the species may therefore involve something more than direct competition.

The planting of exotic species should be stopped. In the present circumstances they represent the most serious long-term threat to the survival of C. rhothophilum. If serious wind erosion problems exist, it would be preferable to handle them with totally artifical methods until the native vegetation can be re-established.

Future development should be carefully planned with respect to dune growth and movement. Proper siting and caution in construction should eliminate the need for special dune stabilization efforts.

Studies should be done to determine the rate of spread of the existing stands of European beach grass. If the rate of spread is significant, control measures should be considered.

7.4 Continue the policy of strictly limited dune access and recreational use

Dune vegetation is adapted to a physically stressful environment and has a considerable ability to recover from disturbance. But continual heavy use of an area by pedestrians or vehicles will eventually eliminate all but a few species, as may readily be observed at Pismo Beach. C. rhothophilum is likely to be particularly sensitive to trampling. The plants have large succulent leaves that are easily bruised and broken. Seedlings could be killed by a single step. Plants can be undercut or buried if dune slopes are disturbed.

Because of the damage caused to the vegetation and the potential impact on least terns, the ban on vehicle use in the dunes should be continued. Access by foot is a lesser threat and does not need special regulation as far as plants are concerned at this time, but the situation should be regularly evaluated.

7.5 Maintain a conservative management policy toward Cirsium rhothophilum and other potentially and endangered dune species

The highly clumped distribution of C. rhothophilum and its absence from many seemingly favorable habitats suggests that its population size could be increased by artificially dispersing seed. While this probably would work, there is no assurance that this might not do more harm than good by depleting seed supply in the best habitat. There is even less assurance that if it were successful in increasing population size that the increase would be more than temporary. Though the present population is clumped, the clumps are widely distributed, and there is no evidence whatever that the total population size is nearing a critical minimum.

However, if any local population were to be destroyed by base development, an effort should be made to salvage at least the seeds. These could then be planted in a variety of suitable habitats. For the reasons stated above this would not probably compensate for the loss of habitat, but it would be an inexpensive procedure that might produce at least a short-term benefit.

At present the active measures to be taken to insure the survival of C. rhothophilum and its associated species are the ones outlined in Sections 6.3 and 6.4--limit access to the dunes and stop the planting of exotic species.

7.6 Re-evaluate the status of C. rhothophilum in the future

The present survey suggests a large and stable population, but the introduction of exotic species, possible impacts of human use, and future developments may alter the situation. A broad survey to estimate density of Cirsium rhothophilum should be conducted in five to ten years.

APPENDIX A

Abundance and distribution of _Cirsium rhothophilum_ on Vandenberg AFB.

INTRODUCTION

Cirsium rhothophilum, the Surf thistle, is an inhabitant of the coastal strand dunes of northern Santa Barbara county. Since it is restricted to moving or only partially stabilized dune areas, the recent pressure of recreational use in these areas accessible to the public has greatly limited the available habitat for the plant. Estimates of its numbers are sufficiently small to have warranted its inclusion on the California list of rare and endangered plants.

Vandenberg Air Force Base encompasses an estimated 6.14 square kilometers of sand dunes that have so far been little affected by development or vehicle traffic. These dunes provide a protected refuge for _Cirsium rhothophilum_ where natural populations of the plant can be studied in a more or less undisturbed state. It was the purpose of this project to gather information about the extent of _C. rhothophilum_ populations in the VAFB dunes, and estimate its density and numbers. In addition, we sought information on the specific habitat requirements of the plant, and on the composition of the plant communities with which _C. rhothophilum_ is associated.

METHODS

Cirsium rhothophilum is a member of the Coastal Stand plant community (Munz 1973) that is found associated with sandy beaches and dunes. In order to characterize the plant species and dune types found in this community on VAFB, a vegetation survey was conducted that encompassed all of Vandenberg's dunes. North VAFB was sampled from Schuman Creek south to about 0.5 km south of Purisima Point. Sampling at South VAFB began about 0.5 km north of the Santa Ynez River mouth and continued south to about 2.5 km south of the river. (Map 1).

The study group was divided into two teams, and sampling was begun at the mouth of San Antonio Creek. One team moved north, and the other worked their way south. Using a compass and a 30 meter fiberglass tape, transects were marked off every 400 meters. The transects were aligned with true East, and extended from the beach over the moving dunes to 60 meters into the stabilized dunes (Figure 1). One square meter quadrats were established every 15 meters along these transects to the north of the tape, and all plant species present inside these quadrats recorded, including seedlings. In addition, each quadrat was characterized by its slope, aspect, type of substrate in which it was located (moving dune, stabilized dune, beach, or open stabilized dune) whether it was to the windward or leeward side of a slope, what percentage of it was covered by vegetation, and its location on a slipface, sand flat, or hollow. A moving dune was defined as a mound of sand upon which plants were established, but no accumulation of organic matter or "soil" was evident. A stabilized dune is a region with a dense covering of plants, including some members of the adjacent Coastal Sage community, where organic matter and soil have mixed with the sand, forming a stable and unchanging substrate. At South VAFB some dune areas, particularly in swales, were encountered that combined features of both of the above dune types, and these areas were characterized as open stabilized dunes. A total of 766 quadrats were sampled in this fashion. A total of 52 species were identified (see attached species list); data for the 10 most common species and their association with Cirsium are summarized in Table 1.

Because C. rhothophilum is too rare to be expected in many quadrats, belt transects were sampled for additional data on this species. A belt was defined along the entire length of all transects, and all Cirsium plants falling within this belt were counted and their locations recorded. (Maps 2-7). The team working to the north of San Antonio Creek sampled a belt 30 meters wide; the team working to the south limited their sampling to a 2 meter wide belt. Estimates of Cirsium density in the dunes are reported in Table 2, as calculated from the quadrat data and from the belt transect data. In addition, Cirsium populations ranging in size from 1-10 individuals up to 100+ individuals have been located and mapped. (Maps 2-7).

RESULTS

From Table 1 it can be seen that C. rhothophilum is associated most frequently with Camissonia cheiranthifolia, Carpobrotus aequilaterus, and Ambrosia chamissonis. These three species are among the most frequently encountered inhabitants of the moving dunes; and, are not generally found in stabilized dune areas. Cakile maritima and Abronia latifolia are also species restricted to the moving dunes. Eriogonum parvifolium and Corethrogyne filaginifolia, in contrast, are stabilized dune species, and were never

	Carp. aeq.	Cam. cheir.	Cak. mar.	Dud. caesp.	Hap. eric.	Core. fil.	Amb. cham.	Hap. ven.	Abron. lat.	Erig. parv.	Cirs. rho.
Carpobrotus aequilatera	226										
Camissonia cheiranthifolia	99	122									
Cakile maritima	41	27	105								
Dudleya caespitosa	60	27	5	68							
Haplopappus ericoides	48	19	1	27	62						
Corethrogyne filaginifolia	53	28	2	35	22	63					
Ambrosia chamissonis	50	40	35	2	4	2	81				
Haplopappus venetus	55	32	9	13	14	6	15	60			
Abronia latifolia	27	46	22	8	4	6	20	15	55		
Eriogonum parvifolium	42	18	4	21	19	24	4	10	6	49	
Cirsium rhothophilum	8	7	2	2	2	0	5	2	2	0	9

Total Quadrats 766

Associations of the 10 most frequent species and Cirsium.

Table 1. Occurrence and co-occurrence of species based on 766 $1m^2$ quadrats placed in the dunes. Values in the diagonal are total occurrence of the species; off-diagonal elements are joint occurrences. For example, C. rhothophilum occurred in 9 quadrats and was found with Carpobrotus aequilaterus in 8 quadrats.

encountered in the same quadrat with C. rhothophilum. We conclude, then, that C. rhothophilum is restricted to moving dunes.

The density estimates for C. rhothophilum on Vandenberg AFB are 82-85m^2 per plant. These estimates were arrived at independently by the use of belt transects and quadrat data, so we feel that they are probably accurate. According to the quadrat data, Cirsium is the least commonly encountered of all the moving dune plants identified (see species list).

Taking the area at the active dunes as 6.14 km^2. the total population of C. rhothophilum is estimated to be between 72 and 75 thousand individuals. Using the slightly greater estimate of 6.72 km^2 of sand dunes given in Coulombe and Cooper (1976) gives estimates of 79 to 82 thousand individuals. We consider the first estimate to be more accurate.

Table 2. Density and estimated population size of *Cirsium rhothophilum* on Vandenberg AFB. Densities are expressed as plants/ha. To get plants per acre, divide by 2.47. The figures apply to the area of moving dunes only.

	Area sampled (m^2)	Number of *C. rhothophilum*	Estimated Density (Plants/ha)
Belt transects	137,520	∿1685	122
Quadrats	766	9	118

APPENDIX B

The population ecology of a rare dune thistle, Cirsium rhothophilum on Vandenberg AFB.

INTRODUCTION

Cirsium rhothophilum, the Surf thistle, is among the most distinctive members of its genus. It is geographically restricted, and occurs only in dunes scattered along a 70 km stretch of the California coast from Point Conception in Santa Barbara County to southern San Luis Obispo County. It is genetically isolated, and is classified as the single species in the subsection Mastigophyllum in the large sub-genus Eucirsium (Owenby et al. 1975). It morphological features suggest a long period of evolution in sand dunes, and it has been described as a good example of rarity brought about by specialization to an unusual substrate. (Raven and Axelrod 1978).

Because of its rarity and biological interest, C. rhothophilum is being considered for legal recognition under federal and state laws protecting rare and endangered plant species. It has been the policy for federal agencies to treat all proposed species as if they have full protection. This means that developments and land use practices on federal property have taken special precautions to minimize harm to designated taxa. It is possible that some projects could be halted entirely if they were judged to present serious danger to the continued existence of a legally recognized rare plant.

Vandenberg AFB in Santa Barbara County California contains a large proportion of total population of C. rhothophilum. The stimulus for this study was the need for information on which to base management decisions. From a practical point of view the main goals of the study were to determine the abundance of C. rhothophilum on Vandenberg AFB, to predict population trends, and to make preliminary judgements about the sensitivity of the species to human activity. While the importance of long-term observations in meeting these goals was recognized, practical contraints required that there be at least tentative answers in a single year's study.

From a more theoretical point of view the problem concerns the probability of local and global extinction of a species occupying a dynamic and in many ways stressful environment. Because C. rhothophilum is short-lived, its populations might be expected to be particularly volatile. But it is also highly specialized to the dunes, and adaptation to a particular environment is unlikely to develop if a species continually undergoes local extinctions and wide swings in abundance. C. rhothophilum may be a well adapted specialist with a prospect of survival identical with that of its habitat, or it may be a faded opportunist limited to a last refuge, and doomed to extinction without active management to eliminate competitors and structure the environment in its favor.

THE STUDY AREA

This study was conducted on Vandenberg AFB in the dunes lying between Point Arguello to the south and Point Sal to the north (see Figure 1). Cooper (1967) divided these dunes into two systems. The southern and smaller he called the Santa Ynez dunes after the Santa Ynez River which enters the ocean near their northern boundary. These dunes are mostly a narrow fringe along the coast lying between the beach and a low cliff of poorly consolidated sandstone of Pleistocene age. In a few places the cliff has been breached and the beach dunes merge with reworked sand from older deposits. In this area the C. rhothophilum populations occur on the leeward side of a single generally continuous transverse dune.

The northern Purisima Point dunes are much more extensive, and include two distinctive geomorphological units representing at least two phases of dune building. The present active dunes have a maximum width of just over a kilometer. Inland from the active dunes is a larger area of older dunes stabilized with a thin cover of open coastal sage scrub. A number of blow out areas, probably resulting from human disturbance, occur at several places. The stabilized dune areas presumably were active in a Pleistocene interglacial period when sea level was relatively high, but lower than it is at present.

Bowman and Inman (1966) calculate that about 38 thousand cubic meters of sand are added annually to the Purisima Point dunes, and about 23 thousand to the Santa Ynez dunes. Assuming that all of the sand is deposited equally over the area of active dunes (estimated to be 6.14 square km) there would be an average increase in elevation of about 1 cm per year. The distribution of sand is of course very unequal, so that particular areas will show net losses and other areas will show gains much in excess of 1 cm.

The Purisima Point dunes are also slowly moving inland. Calculations based on air photos from 1962 and 1975 show that the one kilometer stretch of active dunes just north of San Antonio Creek moved inland an average of 30 meters

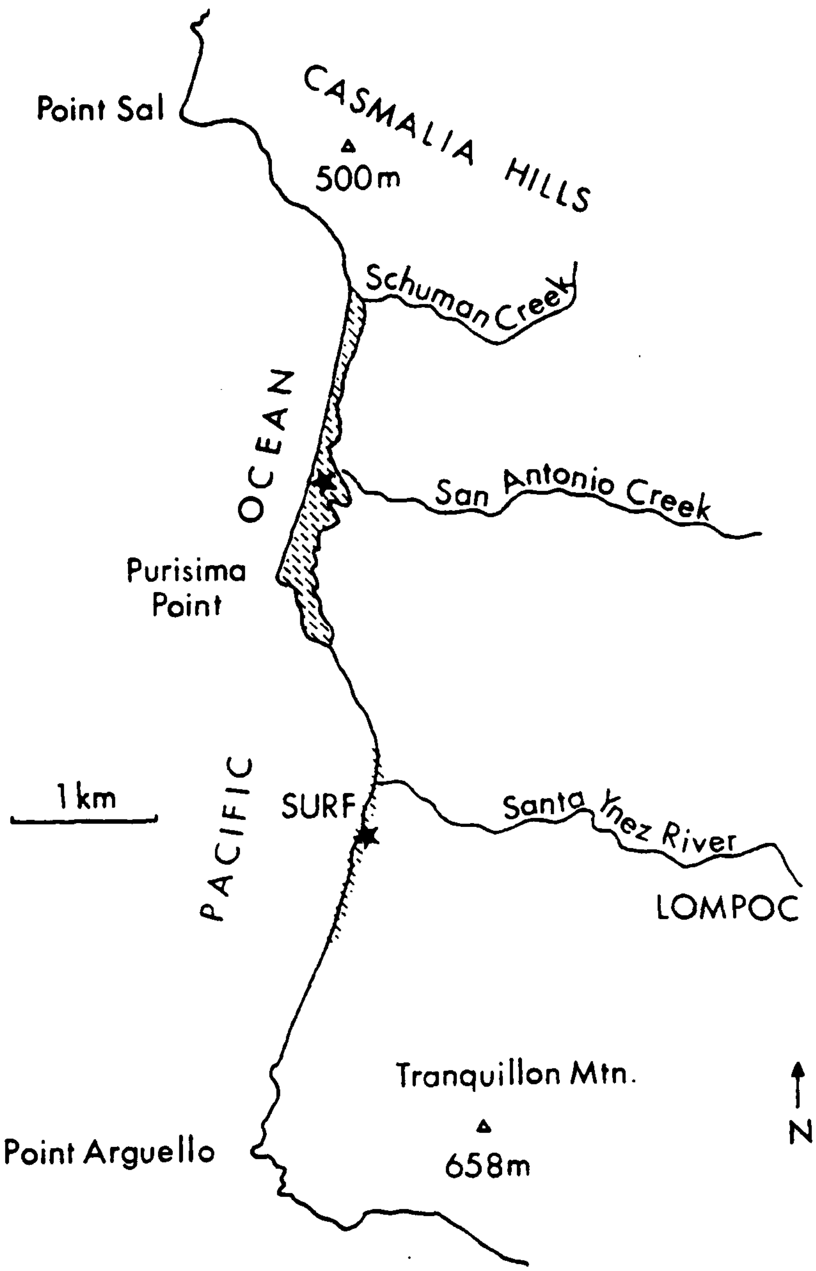

FIG. 1. Location map for the dune study. The area of active dunes are indicated by dashed lines, which also show the approximate angle of orientation of the dune features. The two study sites are marked with a star.

in 13 years, for an annual movement between 2 to 3 meters. This is relatively small movement compared to other dunes (Ranwell 1972) and Cooper's (1967) opinion that the Vandenberg dunes are quiescent seems justified. A limited set of data on sand accumulation and loss in the vicinity of C. rhothophilum populations will be discussed below.

The study areas lies within the Mediterranean climate zone of southern California, with moderate temperatures and a pronounced summer drought. A twelve year weather record is available from the base airfield located about 3 km southeast of the northern permanent transect site at an elevation of about 112 m (U. S. Dept. of the Air Force, 1977). The average mean monthly temperature was 12.8°C with little variation within the year, the highest mean monthly temperature being 15.5°C for October, and the lowest 10.6°C for January. The extreme minimum recorded was -3.3°C in December, and the extreme maximum 37.8°C in September. Annual rainfall averaged 32.3 cm, with the five months from May to October accounting for only 8 percent of the total precipitation. Fog is frequent, especially in the summer and fall months, and when wind-driven off the ocean can sometimes produce substantial fog-drip.

Winds are steady but usually moderate, averaging 11.3 km per hour and coming primarily from the northwest. Gusts in excess of 51 km per hour were recorded in every month of the year, the maximum gust recorded being 75.9 km per hour. Strong east winds comparable to the Santa Ana winds further south occur occasionally, and since they blow contrary to prevailing winds and are often intense; they may be disproportionately important in shaping the dunes.

The topographic features of the dunes, especially in the Purisima Point area, are strongly oriented. Cooper (1967) reported the average direction of the dunes to be N 42 W. Viewed from the air, the dunes give the impression of a series of narrow ridges superimposed on a windswept surface which rises gradually to an average maximum height of about 30 m. The Santa Ynez dunes, which are only a narrow strip for most of their length, have a correspondingly simpler structure.

Before the Second World War, this area of California was not densely populated, and human impact on the dunes was probably light, resulting mainly from cattle grazing and agricultural activity along the margins. During the Second World War, the land was acquired for a military base when the dunes were used for maneuvers. Since the 1950's, the dunes have been part of a missle base, and the level of activity away from developed installations has been much lower. In recent years impacts have resulted from dune stabilization and the recreational use of the dunes by base personnel. Access is now more strictly controlled, in part because of the presence of nesting colonies of the least tern. But despite a long history of human use, the dunes on Vandenberg AFB are probably the least disturbed of the major dune systems in the southern half of California.

METHODS

Field studies were carried out between the 1 June 1978 and 1 August 1979. Fourteen permanent transects, twelve in the Purisima Point dunes, and two in the Santa Ynez dunes were established (see Figure 1). Dunes supporting populations of _Cirsium rhothophilum_ were subjectively selected, starting points randomly positioned, and one meter wide belt transects run with the long axis of the dune. Ten of the transects were 30 meters long, and the other 25, 21, 8, and 4 meters long for a total sample area of 358 square meters.

Within the plots, the location of each _C. rhothophilum_ plant was recorded by X-Y coordinates. Determining the individuality of plants proved to be a problem. A majority of the non-flowering plants have distinct rosettes with a single growing point. These were recorded as "single apex" plants. But other clumps of leaves cannot be easily resolved into separate individuals because of sand burial and sub-surface branching. Excavation of clumps outside of the plots showed that most were single branched individuals. A small number were actually groups of several plants. Because excavation was too disruptive to allow every clump to be checked, all clumps that had the appearance of a single individual were designated multiple apex individuals. The individuality of flowering plants could be determined much more easily, and did not present a significant problem.

Each _C. rhothophilum_ plant located in the transect was classified in one of three mutually exclusive categories 1) flowering individual, 2) non-flowering individual with mature, lobed foliage, or 3) non-flowering individual with unlobed juvenile foliage. The non-flowering individuals were also classified as either single or multiple apex. The following measurements were made on single apex non-flowering individuals: greatest diameter of the vertical projection of the rosette measured from leaf tip; greatest rosette diameter perpendicular to the first measured diameter; total height; and the length and width of the longest leaf. Notes were also made on the condition of the plant, especially the features such as insect herbivory and fungal attack that relate to the probability of survival. The same measurements were made on multiple apex individuals except that the diameters were measured on the clump as a whole rather than on individual rosettes, and that the number of apices in each clump was estimated. The permanent plots were sampled three times, July 1978, and in January and July 1979.

A number of reasonable measurements of plant size could be calculated from the data, but the square root of the product of the two diameters (the geometric mean) proved to be the most informative, and will be used in the growth and population analysis. Werner (1975) has shown that rosette size is a good predictor of the probabilities of flowering and death in the monocarpic species Dipsacus sylvestris.

Different measurements were made on flowering individuals. Since they lack a basal rosette, diameter and height measures were based on the vertical projection of the entire plant. Leaf length and width were measured as for non-flowering individuals. Data on flowers were collected by branch. The maximum length and the basal diameter of each branch were measured. A count of flower heads divided them into flowers and buds. Buds were recorded either as normal, destroyed by predation or disease, or aborted. Flowers were classified as fully formed, destroyed by predation or disease. Fully formed heads were separated into flowering and fruiting stages. Mature but non-dispersing fruiting heads were collected from plants outside the permanent transects, and these dissected to determine the number and condition of achenes in the heads.

The cover of all species in the permanent transects was determined by measuring intercepts along one meter transects perpendicular to the baseline of the permanent transects. All of the cover recorded was therefore of individuals in the permanent plots. One 1 m transect was taken every 50 cm along the baseline, so that the total length of cover transect taken in one of the permanent plots was two times the transect length plus one meter. Cover transects were sampled in July 1978 and July 1979.

In July 1978 individuals outside the permanent transect were measured exactly as those in the transects, and the above ground portion of the biomass rosette harvested. The oven dry weight of these was determined to establish the relationship between size measurements and total above ground biomass. Branches of flowering individuals were also collected in July and August 1978 from individuals outside the permanent plots, and information on the length of branches and the number of flowering heads recorded.

RESULTS

Natural History and Phenology.

C. rhothophilum possesses distinctive traits that represent adaptations to the physical stresses of the dunes. The seedlings are bright green and hairless, but as they increase in size they acquire a dense covering of white hairs. Leaves in younger plants are almost entire and planar. As the plants mature, the leaves become deeply lobed with pronounced undulations. These traits presumably are adaptations to sand abrasion and the high light conditions of the dunes, where photosynthesis is unlikely to be energy limited. The armament of the vegetative parts of the plant are modest by comparison to many other thistles, and this can probably be attributed to less intense herbivory in the dunes. The collection of traits just described is strikingly like those of another restricted dune-adapted thistle, *Cirsium pitcherii*, found along the shore of the Great Lakes. The similarity of the two species is strong evidence for the shared traits being adaptive in a dune environment. However, unlike *C. pitcherii*, *C. rhothophilum* has succulent leaves, presumably a feature related to its salinity tolerance.

Young *C. rhothophilum* plants have asymmetrical rosettes with one leaf conspicuously larger than the rest. As the plants increase in size the rosette assumes a more nearly circular outline. An exception to this tendency for increasing symmetry results from sub-surface branching which seems to be caused by insect damage to the growing point and by sand burial. Branched individuals become clusters of usually asymetrical rosettes, the clump as whole being variously shaped. As discussed in the methods section, these branched individuals are treated separately in some portions of the analysis as "multiple apex" individuals.

Flowering plants lack a basal rosette and generally have several low spreading branches, each with several to many clusters of flowering heads. The bushy habit is probably adaptive in a windy environment with a loose substrate, where an erect flowering stalk could be blown over.

C. rhothophilum does not have a well-defined dormant period, though growth slows in winter and rosette size decreases. Like many species in a coastal environment in California, some flowering individuals can be found almost any time of the year, but the period of maximum flowering occurs from late spring through midsummer, late May to late July; and not from April to June as indicated in Munz (1970). Hawk moths were seen visiting the flowers, and considering the white to cream color of the flowers, they may well be major pollinators.

The majority of flowering plants die when flowering is complete. By mid-winter most of the summer-flowering plants are dead and have begun to break apart. Most of the achenes have dispersed by this time.

The mature achenes are similar to those of other Cirsium species. They have a plume-like pappus which is easily detached, and a mean pappus-free weight of 10.6 mg which is heavier than many other Cirsium species (Pigott 1968, Grime 1979). Dispersal peaks in July and August.

Seed germination begins with the winter rains, and continues through the spring. In July 1979 seedlings barely beyond the cotyledon stage were common. In the early stages of growth much of the energy is channeled to root growth, and the maximum depth of rooting of well-established individuals is certainly in excess of a meter. The deep rooting of C. rhothophilum accounts for its ability to remain active through the summer and fall drought.

C. rhothophilum is highly aggregated. Most individuals are located within a few meters of another plant. It does not occur on the beach, and is largely absent from the seaward slope of the first line of dunes. In the Purisima Point dunes, it is mostly found 100 m or more behind the foredunes.

Only one C. rhothophilum plant was located in the older stabilized dunes during the course of the study. This is surprising because in many places large populations of C. rhothophilum occur along the edge of the stabilized dunes.

C. rhothophilum is conspicuously susceptible to a number of insects, but the most destructive appears to be the artichoke plume moth, Platyptilia carduidactylia (Riley). We are indebted to the California Agriculture Department for the determination of this species. The artichoke plume moth is widespread and feeds on a number of species of thistles. It attacks the leaves, buds, and flowering heads of C. rhothophilum. Adult moths emerged in large numbers in the lab from flower heads collected in July 1978, and in the field damage is conspicuous.

Associated Species

Table 1 gives the relative cover of all species encountered in the intercept sampling of the permanent transects. Because the transects were located subjectively in areas with dense C. rhothophilum populations, the data are not representative of the dunes as a whole.

The total living plant cover recorded was 24.9%, the cover of dead plants 2.0%, and of bare sand 73.1%. Barbour and Johnson (1977) report a range of 10-25% cover for exposed sites in the California dunes, with maximum cover up to 50%. According to this, C. rhothophilum occurs in locations that are high in cover for dunes generally, but low in cover for protected sites.

The other species found with C. rhothophilum are mostly those of the active dunes. The majority are perennials or biennials, and many, unlike C. rhothophilum, form mat-like clones by vigorous vegetative spread. Eight of the species recorded (marked with an asterisk in Table 1) are species with maximum abundance in the stabilized dunes. Their presence is evidence of the less extreme conditions of the microsites occupied by C. rhothophilum.

Most of the species are widespread in the dunes of the Pacific Coast (Macdonald and Barbour 1974), but at least two are almost as restricted as C. rhothophilum. Malacothrix incana is found from Ventura County to Pismo Beach in San Luis Obispo County, and Senecio blochmanae from Point Conception to southern San Luis Obispo County (Smith 1976). Dithyrea maritima is more widely distributed, but has not been collected in recent years at many of its former localities, and its present range may be almost as restricted as Cirsium rhothophilum. All of these species are narrow endemics whose recent history may be very similar to that of C. rhothophilum.

Table 1. Relative percent cover of species in the permanent transects based on 329 meters of transect taken in eight of the fourteen transects. Total cover of living plants was 24.9 percent, of dead plants 2.0 percent, and of bare sand 73.1 percent. Nomenclature follows Smith (1976). Species marked with an asterisk are those more characteristic of the stabilized dunes.

	Relative Percent Cover
Ambrosia chamissonis	34.2
Carpobrotus aequilaterus	22.6
Cirsium rhothophilum	13.9
Abronia latifolia	5.1
A. maritima	6.1
Malacothrix incana	2.7
*Happlopappus ericoides	2.5
*H. venetus	2.4
Convolvulus soldanella	2.2
Cakile maritima	2.1
Camissonia cheiranthifolia	1.4
*Eriogonum parvifolium	1.4
*Eriophyllum staechadifolium	1.1
*Senecio blochmaniae	1.0
Suaeda californica	0.5
*Lupinus chamissonis	0.3
Dithyrea maritima	0.3
*Astragalus nuttalli ?	0.1
*Abronia umbellata	0.1
TOTAL	100.0

Population and individual growth.

Table 2, which combines the data from all transects, gives a summary of the population change in C. rhothophilum over the one year of the study. The number of individuals declined by about ten percent from July of 1978 to January of 1979, and then recovered to within five percent of the original value by the following July. The population seems to be dynamic, but relatively stable in numbers. This stability extends to the proportion of the individuals flowering, which was 10% of the total population in July of 1978 and 13% in in July of 1979. The drop in the number of individuals and in the proportion of individuals flowering in January 1979 is accounted for by the fact that late winter and spring is the main season for germination, and late fall and early winter probably the period of maximum mortality, in part because of the death of flowering individuals, few of which survive from July to January.

The estimates of mortality over the three time periods are given in Table 3. Because of minor errors in recording, the number of individuals that are used to calculate mortality was less than the total population known to be present, and calculation of mortality rates from Table 1 will lead to slightly different figures.

Mortality rates are high, with 42% of the individuals dying between July 1978 and July 1979. As pointed out above, the mortality rate in the first period, from July to January is higher than in the second period. A high proportion of the mortality recorded, especially in the first period, is attributable to the death of flowering plants. Between the first and second samples 36 percent of the deaths were those of flowering plants, while in the second period this figure was only 4 percent, and the overall figure from July to July was 26 percent. On an annual basis then, over one fourth of the mortality is the result of the death of flowering plants.

Because of the rather long periods between samples, these are probably minimal estimates of mortality since a certain number of newly germinated seedlings would die without having been recorded. Even disregarding this bias, the mortality rates are high enough to make large oscillations in population size possible if the developmental stage of a large proportion of the population were brought into synchrony. But the large amount of variation in growth rates resulting from microsite differences and chance are probably

Table 2. Population size of _Cirsium rhothophilum_ in the 14 permanent transects, all data combined. The total area of all transects is 358 m^2.

	Time of Census		
	July 1978	Jan. 1979	July 1979
Non-Flowering Individuals			
Initial population	744	---	---
Known new individuals	---	114	183
Surviving from previous period	---	625	501
Flowering Individuals	83	6	99
Total Population	827	745	783
Cirsium density in transects (plants/m^2)	2.31	2.08	2.19

Table 3. Mortality rates for *Cirsium rhothophilum* in the permanent plots between sample dates based on the total sample.

Mortality between	Total Number of Plants Recorded at First Sample	Number which Died in the Interval	Percent Mortality
July 1978 and Jan. 1979	776	221	28
Jan. 1979 and July 1979	720	145	20
July 1978 and July 1979	776	321	41

sufficient to damp the effect of strong year classes.

It was explained in earlier sections that most vegetative individuals are rosettes with a single growing point or apex, but that a certain proportion of the population consists of individuals branched below the surface to form clumps of rosettes. These complex individuals were called "multiple apex" plants. Excavation of multiple apex plants suggested that the branching was induced by damage to the growing point, and that undisturbed development would produce unbranched plants with single apex rosettes.

Whatever the cause, the number of branched plants and the average number of apices of vegetative plants increases as a cohort ages, as is shown in the transition matrix in Table 4 indicating the number of individuals that changed apex number class between July 1978 and July 1979. Because of the sampling difficulties caused by accumulating sand, some of the transitions may be artifacts, but the basic pattern, is clearly toward an increase in apex numbers. Most plants show no change in apex number, but the majority of those that do change show an increase. The 366 plants had an average of 1.26 apices per individual in July 1978. In July 1979 this figure had shown a statistically significant increase to 1.46. As a cohort ages, an increasing proportion of multiple apex individuals is expected. However, as a proportion of the total population, multiple apex plants declined from 211 in July 1978 to 139 one year later. Since it is likely that external and partly chance factors influence branching, this degree of variability is not surprising.

Because there is no simple way to equate the dimensional measurements of single and multiple apex individuals, the more detailed growth analysis will consider only the single apex plants which make up the bulk of the population. In Figure 2 the size-frequency distribution of rosettes for vegetative individuals at the first and second samples is presented. The preponderance of individuals in the smallest size classes fits the pattern expected for a short-lived species in which there is a significant amount of establishment each year. The distributions for the two samples are similar, showing that the population is stable with regard to the relative abundance of size classes as well as in total number of individuals. The size distribution for January 1979, which is not presented here, reflects the general decrease in size of the larger rosettes resulting from the slower growth in winter.

The growth of rosettes between time periods is highly variable. There

Table 4. Change in apex number for non-flowering individuals that survived from July 1978 to July 1979.

Number of Apices	No Apices - July 1979			
July 1978	1	2	> 2	Total
1	257	44	13	314
2	8	11	14	33
> 2	1	4	14	19
TOTAL	266	59	41	366

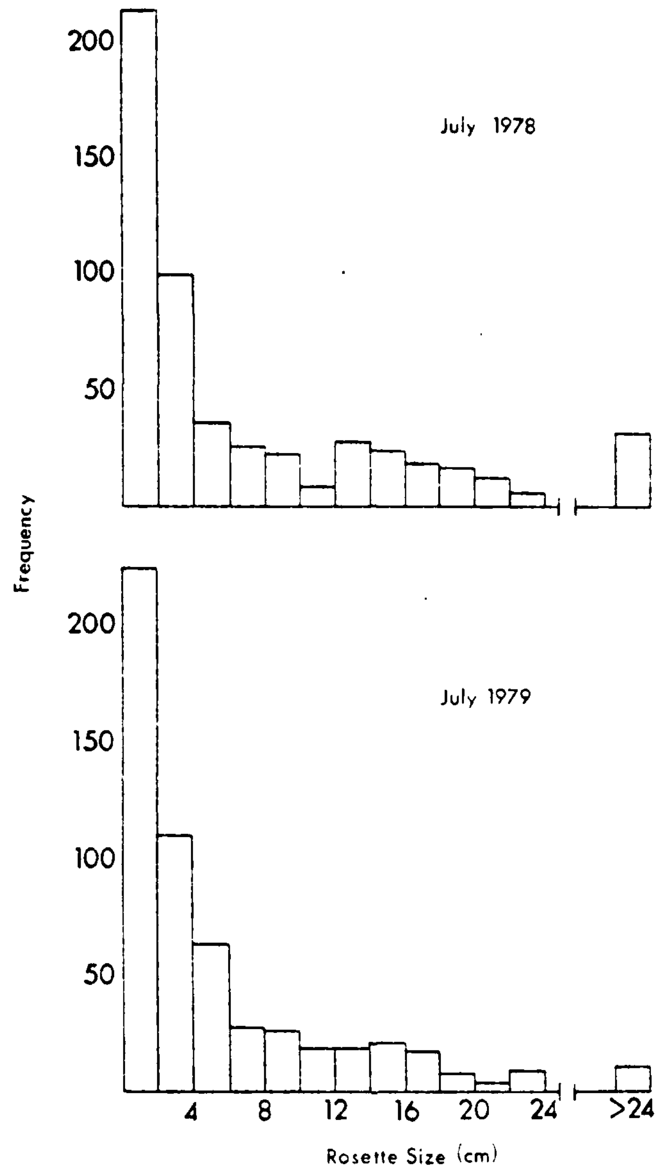

FIG. 2. Frequency distributions for geometric mean rosette diameter for non-flowering single-apex individuals of Cirsium rhothophilum in two years.

is a strong seasonal pattern, with the rosettes shrinking in size in the winter and then recovering in the spring and summer. Further variation is caused by the attacks of insect herbivores and by the burial by moving sands. Rosette size at the time of one sample proved to be only a fair predictor of rosette size at the next sample even when these predictions were made from July to July to eliminate the effect of seasonal variation. A large proportion of rosettes actually decreased in size.

The highly variable growth patterns are readily apparent in Table 5 which shows, for single apex plants only, the size transitions of vegetative plants recorded in July 1978 and July 1979. Rosette growth could not be measured if a plant died or flowered in the interval, and these plants are classified in the appropriate categories in the right hand columns. The data show that most plants stayed in the same size class or moved to a larger size class, while others showed large decreases in rosette size. Growth of the vegetative rosette in C. rhothophilum is not necessarily an orderly process of steadily increasing size.

The growth data are presented in a slightly different way in Figure 3. The non-flowering single apex rosettes that survived in the non-flowering state to July 1979 were divided into rosette size classes. In order to make the number of observations in each interval more equitable, unequal size classes having broader ranges in the largest classes were used. The average size of the individuals in each size class in July 1978 was calculated, providing the X coordinate for each point, and then the average size of the same collection of individuals one year later was calculated to give the Y coordinate. The scatter of points represents a smoothed set of data relating the size of a rosette in July 1978 to size in July of the next year. The time period between samples was 0.94 years. The bars plotted about each point are two standard deviations of the mean. The confidence one can place in size predictions decrease with increasing rosette size, partly because of smaller sample sizes, but primarily because of increased variation in growth patterns.

The curvinearity of the points with respect to the dashed line of no difference implies that growth rises to a maximum and then declines with the largest class of rosettes actually having negative average growth. From these data it would appear that C. rhothophilum rosettes tend to approach a maximum size, though the high variability means that this maximum is not a fixed figure.

Table 5. Single apex rosette size class transitions, July 1978 to July 1979. The columns labelled "Flow." and "Died" record the numbers of plants that flowered and died, respectively.

Initial Size Class (cm) July 1978	Final Size (cm) July 1979									
	0-2	2-6	6-10	10-14	14-18	18-22	> 22	Flow.	Died	Total
0-2	39	58	9	7	0	0	0	2	96	211
2-6	3	21	19	12	10	1	0	4	61	131
6-10	1	3	4	5	13	0	0	2	18	46
10-14	1	0	3	5	6	2	6	3	10	36
14-18	0	1	0	1	5	4	4	7	8	30
18-22	0	1	0	1	0	2	5	9	11	29
> 22	0	0	0	1	0	1	3	15	14	34

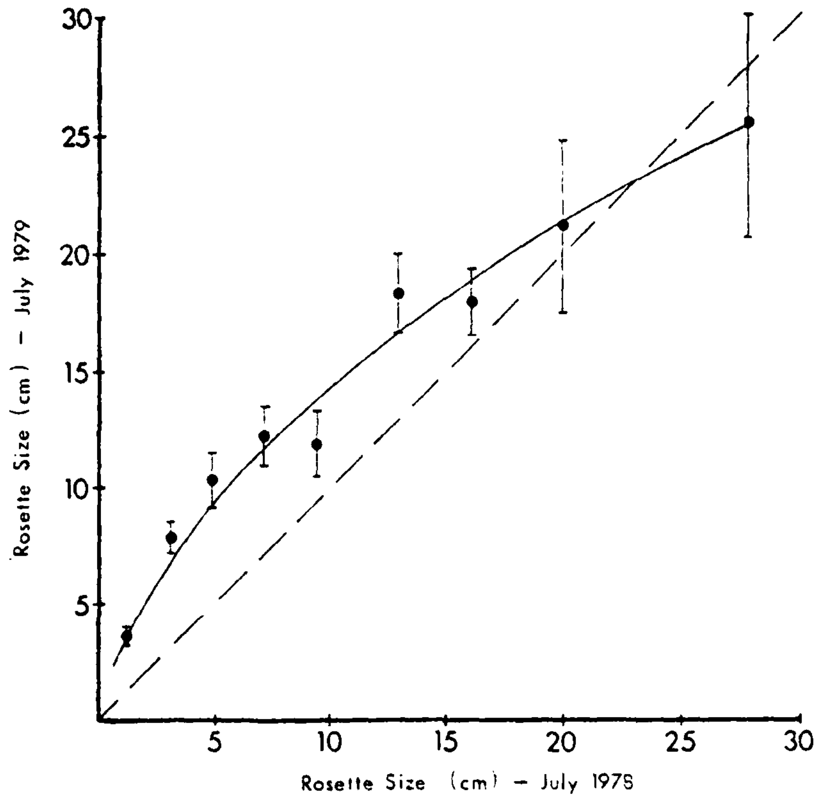

FIG. 3. Smoothed data giving the relationship between rosette size (geometric mean diameter) at the first and last sample. Data points are averages by size groups. Vertical bars are two standard deviations of the mean long. The dashed line is the line of no difference. The solid black line is a regression line derived by an iterative procedure to derive the parameters for the Richards growth function.

The data plotted in Figure 3 can be used to derive a growth curve if the assumption is made that the growth observed in this time interval for each size class is representative. The parameters of the Richards growth curve (Richards 1959) can be obtained from a regression line fitted to the data of Figure 3 after a suitable transformation. Richards' function is a general growth curve which includes as special cases the logistic, Brody-Bertalanffy, and Gompertz equations and has the form:

$$S_t = S_\infty (1 - be^{-kt})^{-n}$$

The derivation of the parameters S_∞, n, and k was facilitated by use of a computer program and accompanying documentation written by T. Ebert.

The way the parameters are derived is made more clear by an alternative expression of the function which relates size at two times, t and t + T, where T is the time increment in appropriate units:

$$S_{t+T}^{-\frac{1}{n}} = S_\infty^{-\frac{1}{n}} (1 - e^{-kT}) + S_t^{-\frac{1}{n}} e^{-kT}$$

This expression gives transformed size at the second time as a linear function of size at the first time with slope e^{-kT} and intercept $S_\infty^{-\frac{1}{n}}(1 - e^{-kT})$.

Given values of n and T, it is possible to calculate values of the growth constant k and the maximum size S_∞ from the slope and intercept of a linear regression of transformed size measurements. The best value of n was determined by an iterative procedure that minimizes the residual sum of squares calculated on the basis of differences between the untransformed values of final size and predicted final size estimated by the regression equation.

The fitted curve is shown in Figure 3 as the solid line. It accounts for a major part of the variation in ordinate values. Deriving the value of k and S_∞ from the regression, taking the value of n as 7.26, and estimating the time interval as 0.94 years gives the growth curve in Figure 4.

As expected from the curvilear pattern in growth discussed earlier, the growth curve exhibits a pronounced levelling and approach to an average maximum size. The time to reach average size is surprisingly long, and the growth curve indicates that C. rhothophilum is a short-lived perennial rather than a biennial. The large variability in growth evident in Table 5 requires

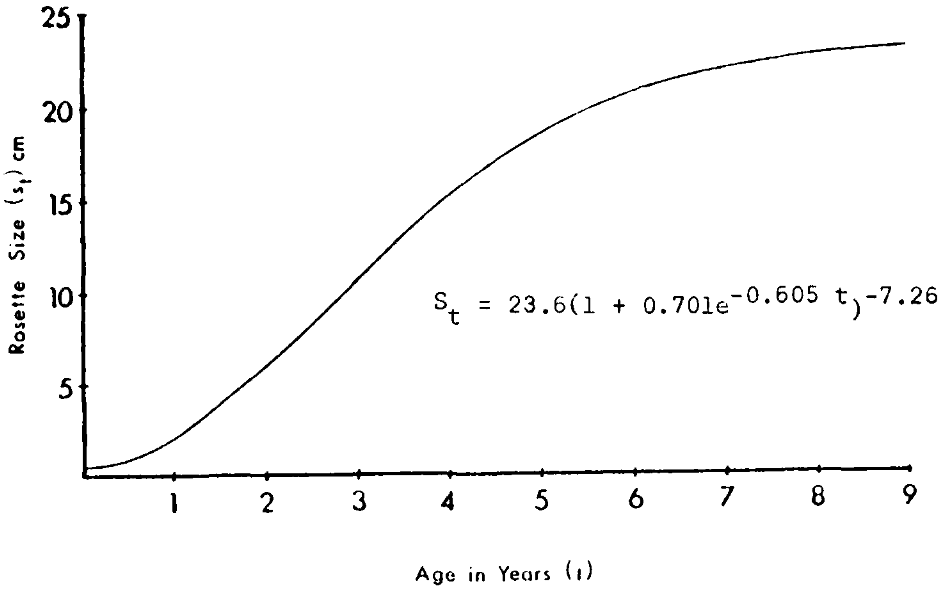

FIG. 4. Growth curve for single-apex rosette diameter calculated from the data given in Fig. 3.

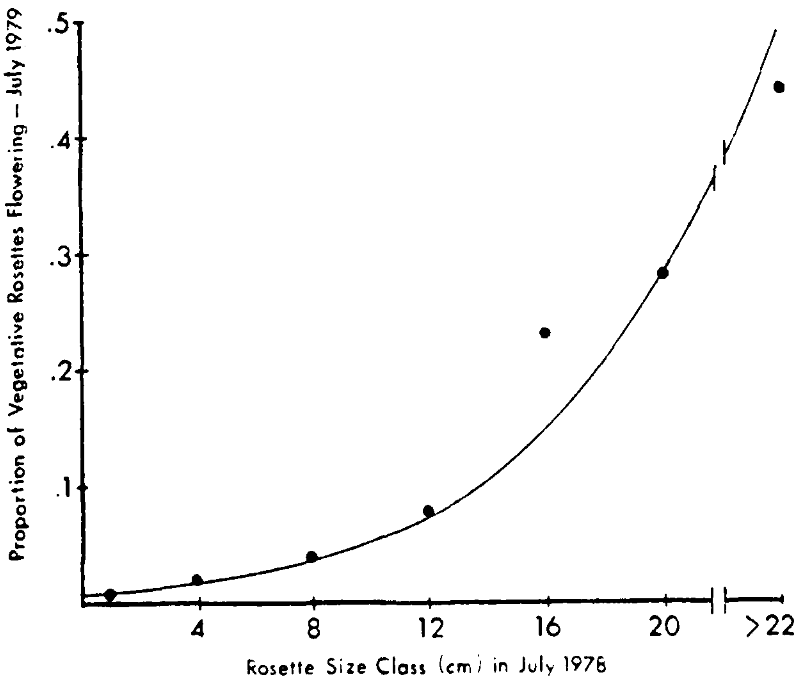

FIG. 5. The proportion of rosettes flowering in July 1979 plotted against rosette size class in July 1978. The solid line is a fitted log-linear regression line significant with $P < 0.001$.

that the curve be regarded as an estimate of an average rosette growth pattern.

Because most C. rhothophilum plants die after flowering, the size related probability of flowering can be used together with the growth curve to estimate longevity. In Figure 5 the proportion of single-apex rosettes measured in July 1978 that flowered in July of 1979 in each rosette size class is plotted against the midpoint of the size classes. A statistically significant relationship results, with the proportion of flowering plants increasing sharply with increasing rosette mean diameter. Combining the information in this graph with the estimated average growth curve leads to the prediction that many rosettes do not initiate flowering until they are more than six years old. The average rosette size in July of 1978 of individuals that flowered in July of 1979 was 18.4 cm, a size corresponding to a predicted age of about 5 years. According to this, the average individual flowers in its sixth year.

While we can think of no reason why the data should be biased in the direction of underestimating growth rates or overestimating the age of the rosettes, the predicted times to flowering seem high. But neither field observations nor other independent data are inconsistent with the prediction of relatively long life. Werner (1975) found that Dipsacus sylvestris, usually classified as a biennial, commonly lived for more than two years with flowering more dependent upon accumulated reserves, and therefore size, than on chronological age. It is possible that C. rhothophilum is a biennial under ideal circumstances, but longer lived in the stressful environment of the dunes. Since hypothetical behavior in ideal conditions is not a useful basis for an ecological classification of life history, it is appropriate to consider C. rhothophilum to be a short-lived monocarpic perennial.

But the monocarpy is not absolute. We found several plants that resprouted after flowering. Four flowering plants, or about 4% of the total number that had flowered in July 1978 had produced small vegetative sprouts in later samples. The new shoots were small and their fate is uncertain. Resprouting could perhaps be a heritable trait of low frequency, but it is more likely stimulated by injury or other growth anomalies. Harper and Wood (1957) report that this is the case for a monocarpic Senecio.

The prediction of a long time to flowering is given indirect support by the large size of flowering plants, and the large amount of stored energy that must be required to produce them. Flowering plants had an average of 3.4 branches per plant, with the largest individuals having up to 18 branches and maximum crown diameters in excess of 1 m. Table 6 gives the breakdown by major component of flowering individuals collected near the end of the flowering season in July 1978. The average oven-dry weight of the above-ground biomass of a sample of 16 flowering individuals was 166 gm, with a maximum of 453 and a minimum of 5.9 gm. As might be expected, a substantial proportion of the biomass, about 38% of the total, was in flowering and fruiting structures.

Flowering, seed production, and germination.

The number of flower heads produced by an individual plant is highly variable, as is evident in a frequency distribution of number of undamaged flowering heads per individual (Figure 6). The largest plants contribute disproportionately to achene production. One plant observed in July 1978 had 222 fully formed flowering heads, equivalent to an estimated 2200 viable achenes, and a potential achene production six times this.

In July of 1978 seed heads were collected from plants outside the plots and dissected to estimate the potential and actual number of seeds produced. Only fully-formed heads were collected. The heads were taken apart and the achenes divided into three classes: aborted, destroyed by insects, and apparently sound. Since soundness was estimated visually, this procedure tended toward a maximum estimate of viable achenes.

The results of the dissection are shown in Tables 7 and 8. Combining all of the data gives an estimate of 77.2 for the average number of potential achenes per head, while the average number of sound achenes per head was estimated to be about 13, only 17% of the total potential achenes.

Insect predation, primarily attributable to the artichoke plume moth, is a major and readily identifiable cause of achene loss. Based on a sample of more than 8000 seeds, insect damage was estimated to destroy about 16 percent of the achenes. This is certainly an underestimate since it does not include aborted achenes that did not develop because of insect feeding. It also does not include the effect of insect feeding on immature heads. The combined data from all three samples indicates that 618, or 11% of the flowering heads and buds counted on flowering plants were destroyed by insects. Considering

Table 6. Oven-dry weight of various above-ground plant components for flowering *Cirsium rhothophilum*. Figures are percentages of total average weight ± one standard error of the mean expressed as a percentage. Table is based on dissection of 16 individuals having a total of 81 branches. Average total above-ground biomass per individual was 166 gm, with a standard deviation of 127 gm. Plants were collected in July 1979 near the end of the flowering season.

Component (% of total dry weight)				
Stems	Leaves	Undamaged Flowering Heads and Buds	Undamaged Fruiting Heads	Damaged Heads and Buds
29 ± 6	33 ± 6	2 ± 0.5	27 ± 4	9 ± 0.7

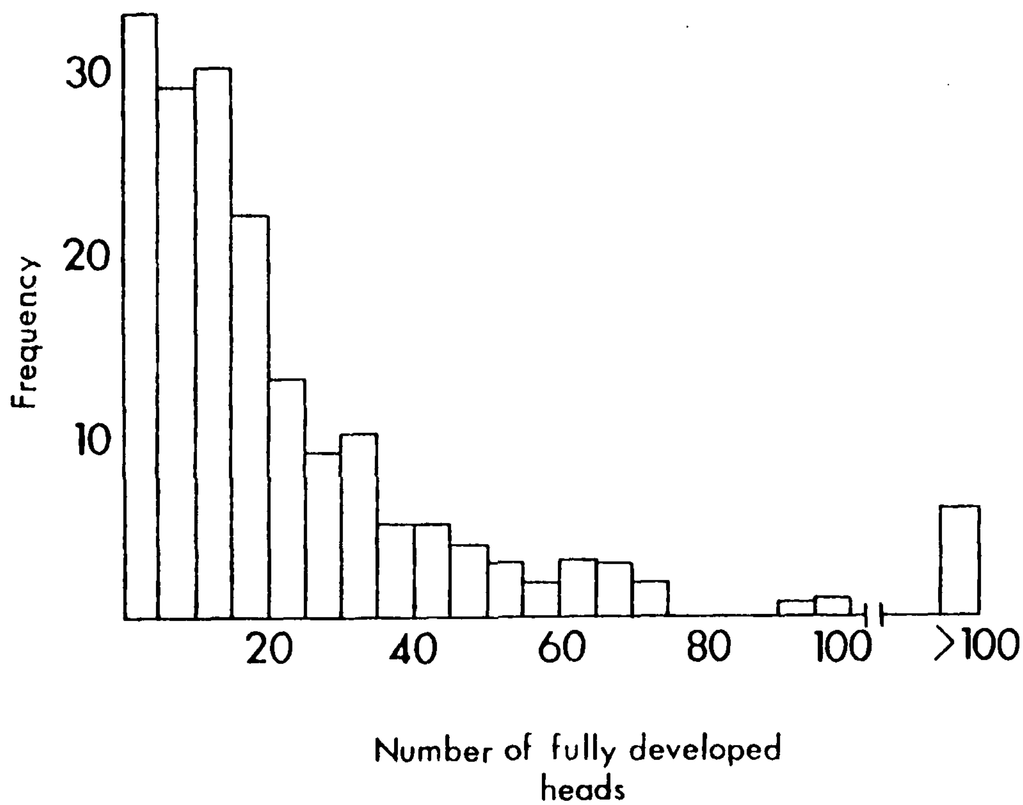

FIG. 6. Frequency distribution giving the number of Cirsium rhothophilum plants having different numbers of fully formed flowering heads. Total number of flowering individuals measured was 186.

Table 7. Estimated achene production of Cirsium rhothophilum on a per head basis for randomly selected heads collected in July 1978.

	ACHENES/HEAD $\pm S_{\bar{x}}$	N
FULLY FORMED, UNDAMAGED ACHENES	13.1 ± 1.1	208
TOTAL ACHENES, POTENTIAL AND FULLY FORMED	77.2 ± 3.2	108

Table 8. Achene condition in Cirsium rhothophilum as estimated from 108 fruiting heads collected in July 1978.

	N	%
SOUND	1845	22
DESTROYED BY INSECTS	1346	16
ABORTED	5161	62
TOTAL	8352	100

both levels of damage, the heads destroyed and the seeds within fully formed heads destroyed, gives a minimum estimate of 25% destruction of the potential achene crop by insects. This is moderate predation compared to the rates ranging between 35 to 73% observed by Louda (1978) in the perennial polycarpic composite species *Happlopappus squarrosus* and *H. venetus* near the coast in San Diego County. But *C. rhothophilum* is much rarer than either of these species, has a much lower total seed production per plant, and is monocarpic. Considering this, the insect predation even though less intense, would probably be more important in determining population size.

Flower production measured at the two July samples was remarkably similar, further evidence in support of the idea that *C. rhothophilum* populations are relatively stable. Total flower production for all transects combined in July 1978 was 2937 flowers, of which 2255 were classified as fully formed, while the corresponding figures for July 1979 were 2764 with 2200 considered fully formed. Assuming that the dissection figures for 1978 are representative, the approximate number of potentially viable achenes produced in the transects is about 29,000 for both years. Using the figures for 1978, this means that there were about 86 achenes available to replace each of the individuals that died.

Breaking the data down by transect and plotting the number of achenes produced in 1978 against the number of seedlings produced in the subsequent samples produced a random scatter of points. This is perhaps not surprising, since the transects are rather artificial sub-populations. The average trends for stability in numbers and flower production may hold even when particular areas show significant increases or decline. Features of the physical environment, especially sand deposition, may be of overriding importance, and may mask relationships between seed input and seedling establishment.

Germination tests to determine the viability of the achenes collected in both years were run in the fall of 1979. In one test achenes were germinated on moist filter paper in petri dishes under a daily cycle of 12 hr. at 20°C in the light and 12 hr. at 15°C in the dark. The cumulative germination curves (Figure 7) show that the older achenes germinated slightly faster and had a higher percentage germination at the conclusion of the test. A Kolmogorov-Smirnov test for equality of distributions confirmed that the normalized curves for different ($P < 0.05$) and therefore that the rate of germination differed, and a chi-square test for equality of proportion germinating shows that the total germination also differed significantly. While statistically significant, the differences are small, and the major conclusion to be drawn is that seed dormancy is at best weakly developed in C. rothophilum. Most achenes that are not destroyed by physical or biotic factors probably germinate within six months of their dispersal. The seed bank in the soil is probably very small except in the period of the year after dispersal of achenes but before the winter and spring rains.

In another experiment, achenes were planted at depths of 0, 0.5, 1, 2, 4, and 8 cm in dune sand, with 100 achenes from each year's collection at each planting depth, for a total of 200 achenes at each depth. The temperature and light regimes were the same as that of the petri dish experiment. The number of seedlings appearing at the surface of the soil and producing normal cotyledons was recorded. The results, combining the two collections, are plotted in Figure 8. Emergence declined exponentially with depth past a depth of 1 cm. A two-way chi-square analysis with depth of planting and year of collection as the factors, indicated that the depth factor was significant with $p < 0.05$, but that year of collection was not.

The high value for the achenes placed on the surface (i.e. 0 cm depth) conceals a significant fact. Although the achenes germinated and produced normal seedlings, none were able to get their hypocotyls into the sand. If the definition for successful establishment were broadened to require implantation, this first data point would drop to zero. There is a minimum as well as maximum depth of burial for successful establishment.

The failure of seeds to emerge from greater depths was not because the seeds did not germinate, but because they were unable to get their cotyledons to the surface. Germination was high in the deeply planted achenes. Van der Valk (1974), in a similar set of experiments with several species from the North Carolina dunes found a strong relationship between maximum depth at which emergence was noted and seed weight.

The data of DeJong (1979) suggest that soil moisture tensions at all depths in the sand would be high for periods long enough to germinate buried C. rhothophilum achenes except perhaps for those buried deeply enough for oxygen to be limiting. Because of the lack of dormancy, the achene reserve can provide little buffering against extinction in the event of an exceptionally bad run of years for adult survival or flower production. A larger proportion of achenes might survive under drought conditions.

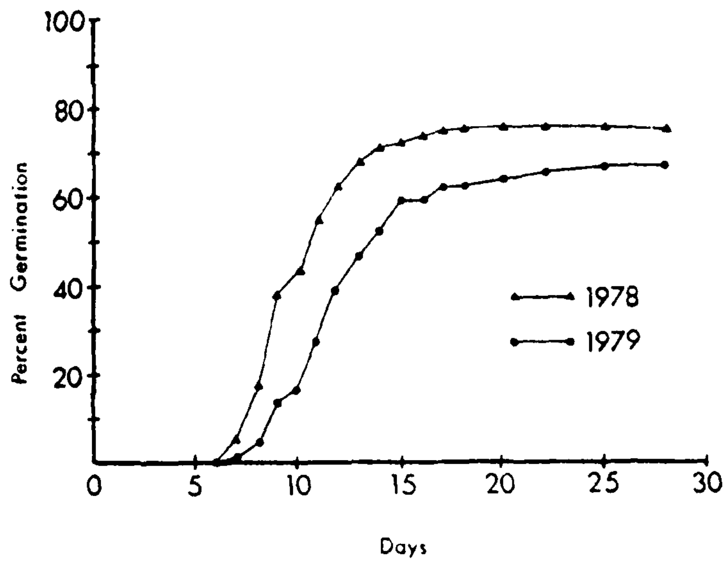

FIG. 7. Cumulative germination curves for Cirsium rhothophilum collected in two years and germinated in the fall of 1979.

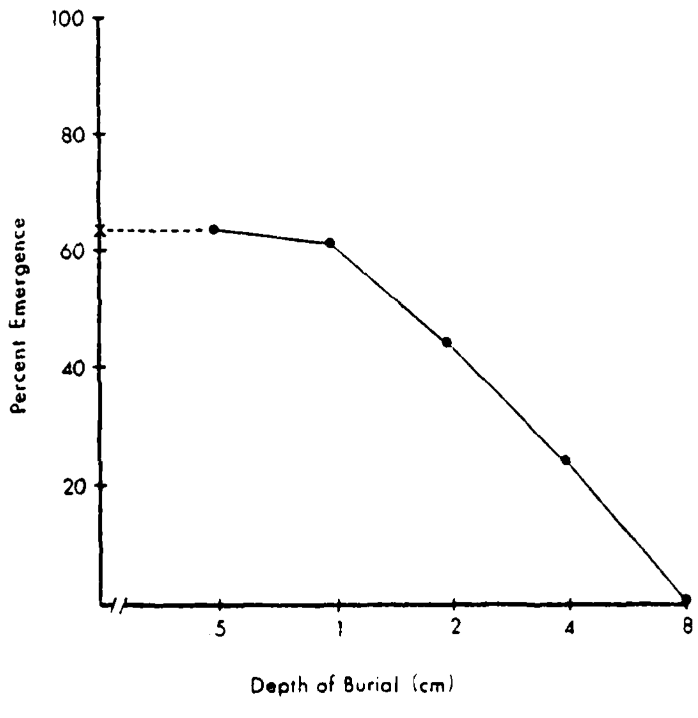

FIG. 8. Proportion of Cirsium rhothophilum seeds emerging from various depths of beach sand. Data are derived from a laboratory experiment. Note the logarithmic scale on the X axis. Two hundred seeds were planted at each depth. The "X" at 0 cm depth is not emergence, but percent germinating. None of the seeds that germinated at the surface became established because their hypocotyls failed to enter the substrate.

DISCUSSION

Cirsium rhothophilum populations showed little change in important population features from July of 1978 to July of 1979. The number of individuals, rosette size distribution, proportion of plants flowering, and flower production were all very similar at the two summer samples despite the relatively high mortality rates. The largest changes were between the summer of 1978 and the winter of 1979, and were due to seasonal patterns of vegetative growth, seedling establishment, and mortality. The limited amount of change in the populations and the relatively long life expectancy of well established plants create the impression of a species which is well adapted to its environment and buffered against year to year environmental variation.

This is perhaps what would be predicted for a rare but specialized plant. Given the small area in which it grows and the resulting small total population size, the species would be unlikely to survive if it typically experienced wide variation in abundance. The major changes in the population size of _C. rhothophilum_ until the last century were undoubtedly the result of changes in the area of active dunes. The recent recreational use of dunes has probably caused a greater reduction in the population than the operation of any natural process since the end of the Pleistocene.

The scattered distribution of _C. rhothophilum_ in the dunes could be taken as evidence that the population is declining, since it occupies such a small fraction of even the most favorable habitats. While this interpretation is superficially reasonable, it is almost certainly wrong. The present distribution of _C. rhothophilum_ in the Vandenberg dunes is probably close to the natural and expected pattern. Three major factors seem sufficient to explain why the population is not more nearly continuous or widespread: 1) the intolerance of _C. rhothophilum_ to the physical conditions in exposed sites, 2) its inability to persist except where the surface is stable or accreting, 3) its limited competitive ability in situations where the substrate is uniformly exploited, and 4) relatively low seed production and strongly directional seed dispersal.

C. rhothophilum is not remarkable in having a highly aggregated population structure. In the dunes of the study area, all of the native species tend to occur in patches. The extreme stresses of the dune environment are well documented (e.g. Barbour 1970a, 1978; Van der Valk 1974, Ranwell 1972) and even the hardiest pioneers show clear signs of stress in exposed locations. No physiological studies on the tolerance of C. rhothophilum to factors like salinity and abrasion have been carried out, but it is doubtful that it has more than average hardiness. For example, its large leaves and deep roots would be disadvantageous in minimizing salinity effects. It is safe to assume that the greater part of the active dune habitat is unavailable to C. rhothophilum as it is to most other species because it is physiologically incapable of growing there.

In active dunes, plants have the problem that the most sheltered sites tend also to be areas of sand accumulation. C. rhothophilum generally occurs in locations that are gaining sand. It is common to find plants buried by sand, but much rarer to find ones that have been excavated. The sand budget in the vicinity of a C. rhothophilum population was characterized by small set of measurements made in the vicinity of the permanent transects in the Purisima Point dunes. In July 1978 eleven iron stakes 1 cm in diameter and 1.2 m long were driven into the sand leaving 15 cm exposed. The arrangement of stakes in relation to the dune is shown in Figure 9. The exposed part of the stakes was measured again in July 1979. The changes in the elevation of the surface in cm are noted in Figure 9.

The dune is moving inland, losing sand from the seaward end and accumulating it at the landward end. C. rhothophilum plants are found on the top and sides of the dune from the third stake at the seaward end to the last stake at the landward end. No C. rhothophilum were growing in the adjacent slack areas. Averaging the change in surface recorded for the six stakes with at least one C. rhothophilum within one meter gave an average change of +2.1 cm, while the corresponding change for the five stakes without nearby plants was -3.0 cm, a difference which is statistically significant with $P < 0.05$.

Sand accumulation presents difficulties for C. rhothophilum, and in the short run it probably represents a stress rather than a benefit. Plants must continually grow to the surface, and this requires energy that could otherwise be channelled into stored carbohydrates to be used in flowering. But burial is better than excavation, which cannot be very effectively countered by normal growth, and which potentially could result in far greater losses of

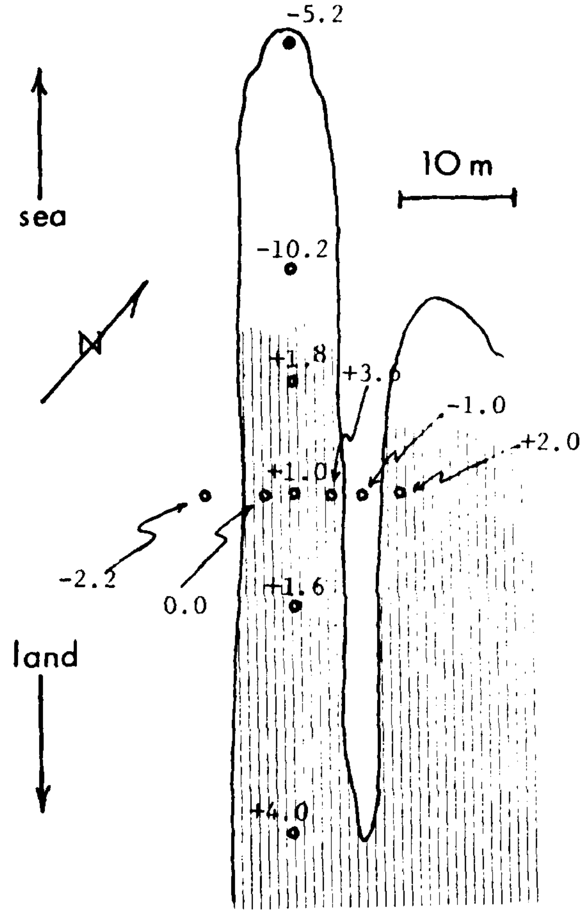

FIG. 9. Change in surface elevation of a dune near the Purisima Point permanent transects between July 1978 and July 1979. The open circles mark the location of steel stakes, and the vertical shading the approximate distribution of Cirsium rhothophilum on the dune. The area pictured lies about 250 meters from the shore.

energy. Similarly, the loss of achenes buried beyond 8 cm is a less serious problem than having seeds swept away entirely.

Despite the difficulties, in the long run, C. rhothophilum is undoubtedly dependent on sand accumulation. Its deep and extensive root system requires a large volume of readily exploited soil of low salinity. Areas of sand accumulation provide an ideal physical environment for root growth, yet prevent even well adapted dune species from fully exploiting the available resources. The longer lived perennials like Ambrosia chamissonis respond more slowly than C. rhothophilum to the creation of new exploitable substrate, and this provides the opportunity for a short lived perennial species to find suitable microsites in the matrix of species that are capable of achieving large size by vegetative growth. If a sand surface is stable for long periods, the cover of the established species will close, and the available habitat for C. rhothophilum reduced.

It is significant in this regard that C. rhothophilum, like Cakile maritima (Barbour 1970b) is very rare in areas dominated by the introduced perennial grass Ammophila arenaria, even in more sheltered places where both species would be expected. C. rhothophilum probably has limited ability to compete against a species that can consistently exploit broad areas of accumulating sand.

While physical factors and competition can explain the absence of C. rhothophilum from much of the dunes, there remain many apparently suitable microsites from which it is absent. Ineffective dispersal may be responsible. Because of the strong prevailing winds, the majority of achenes that move some distance away from the parent plant disperse inland. Points landward of existing populations receive far more achenes than a seaward point at the same distance. Since C. rhothophilum is excluded from the beach and is rare on the foredunes, some otherwise favorable sites probably receive achenes from adjacent populations only in exceptional circumstances. If such sites are large and very favorable, even sporadic dispersal would be enough to insure long-term occupancy, since the local population would either be large enough or vigorous enough to have a low probability of extinction. But smaller or more marginal habitat would require a proportionately higher rate of achene input in order to have C. rhothophilum continually present. A certain proportion of unoccupied habitat is expected.

The absence of C. rhothophilum from the stabilized dunes which lie inland from both the Purisima Point dunes and the Santa Ynez dunes cannot be explained by dispersal. There must be a continual flow of achenes into the stabilized dunes from the C. rhothophilum populations on the margins of the active dunes. While cover is substantially higher in the stabilized dunes, bare patches of sand are not unusual, and blowout areas up to several hectares are present. The failure of C. rhothophilum to exploit small patches of open sand could be explained by competition, but in the larger barren areas of sand this is not sufficient. Herbivory may be important. In the stabilized dunes the work of pocket gophers is very evident, while in the dunes rodent populations of all kinds are much lower. It is possible that C. rhothophilum roots are particularly susceptible, and perhaps sought out by pocket gophers. Predation on seeds after dispersal may also be much higher.

The exclusion of C. rhothophilum may also be partly due to physical differences between moving and stabilized dunes. In the more consolidated and partially weathered soil of the stabilized dunes, root penetration may be inhibited. This, plus increased stress from predation and competition might be enough to make survival very improbable.

Whatever the immediate cause of the restriction of C. rhothophilum, the ultimate cause is certainly the narrow specialization to the dune habitat. C. rhothophilum is genetically unique, and it is reasonable to assume that its specialization is quite ancient. In this it may differ from C. pitcherii, another species of Cirsium found only in sand dunes around the Great Lakes, which is thought to have become genetically isolated in the Pleistocene (Johnson and Iltis 1963). The ecological similarities of these two rather distantly related species is striking. Both are white-hairy deeply-rooted, and monocarpic--all traits of survival value in dunes. The similarity in flower color, both being cream to white, is perhaps accidental. Both species have restricted distribution even within areas of sandy soil. (Johnson and Iltis 1963). In two independent cases specialization to the dunes has had similar consequences for the population ecology of the species.

At the outset of the study we considered it paradoxical that a species should be both very rare and short-lived in a highly changeable environment. We have concluded that the populations might actually be quite stable.

In sand dunes a species that can exploit the open habitat need not necessarily suffer a high rate of local extinction, but the specialization required to achieve long term survival seems to enforce strict limits on local abundance. From a practical point of view, this means that no simple management scheme is likely to increase the population size in a relatively undisturbed dune system. This places a premium on the preservation of as many of the extant populations as possible. It is also very clear that in this, as in so many cases, the only economically feasible way to preserve the species will be to preserve the dune ecosystem in which it is found. This means not only preventing destruction of the area through recreational overuse, but also insuring that the dynamic aspects of dune building on which the species depends are maintained. The preservation of _C. rhothophilum_ and its associated species may require careful evaluation of the effects of development on coastal zone hydrology, especially sand input to beaches and the water table in the dunes.

APPENDIX C

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APPENDIX D

MAPS

The 1st map is an overview of the entire VAFB dune area, with the vegetation survey transects located on it. The scale is 1:50,000. The last 6 maps (2-7) are detailed transect maps including the location of Cirsium rhothophilum populations, identified in 4 size categories. The scale of these maps is 1 cm = 110.78 in.

Legend:

|——| - vegetation sampling transect

------ - boundary of moving and stabilized dunes

++++++ - Santa Fe Railroad

——— - roads, boundaries of military installations

Cirsium symbols:

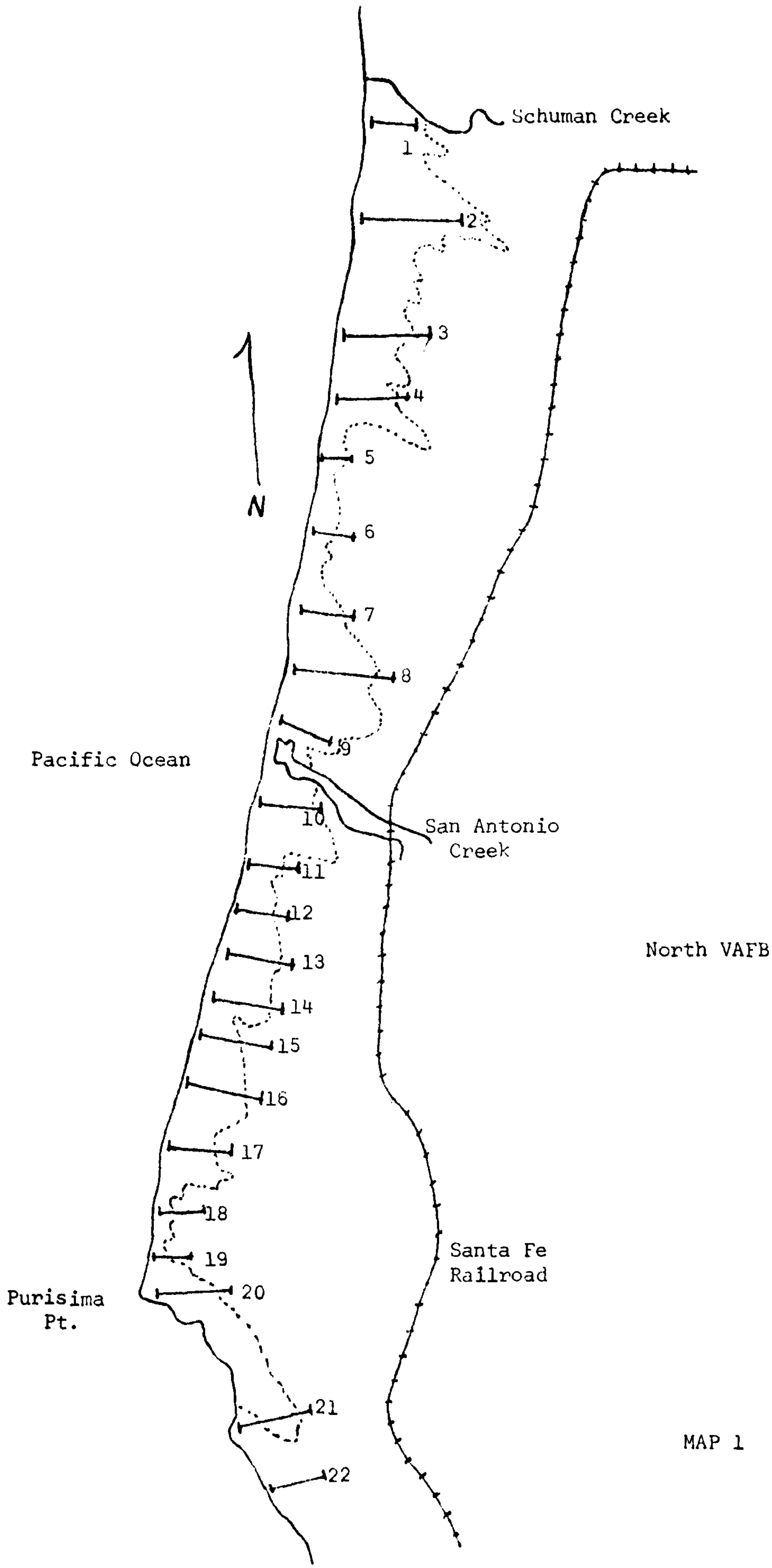
• - Cirsium population of 1-10 individuals

o - Cirsium population of 11-50 individuals

◐ - Cirsium population of 51-100 individuals

● - Cirsium population of 100+ individuals

X - Cirsium plant located in sample quadrat



Schuman Creek
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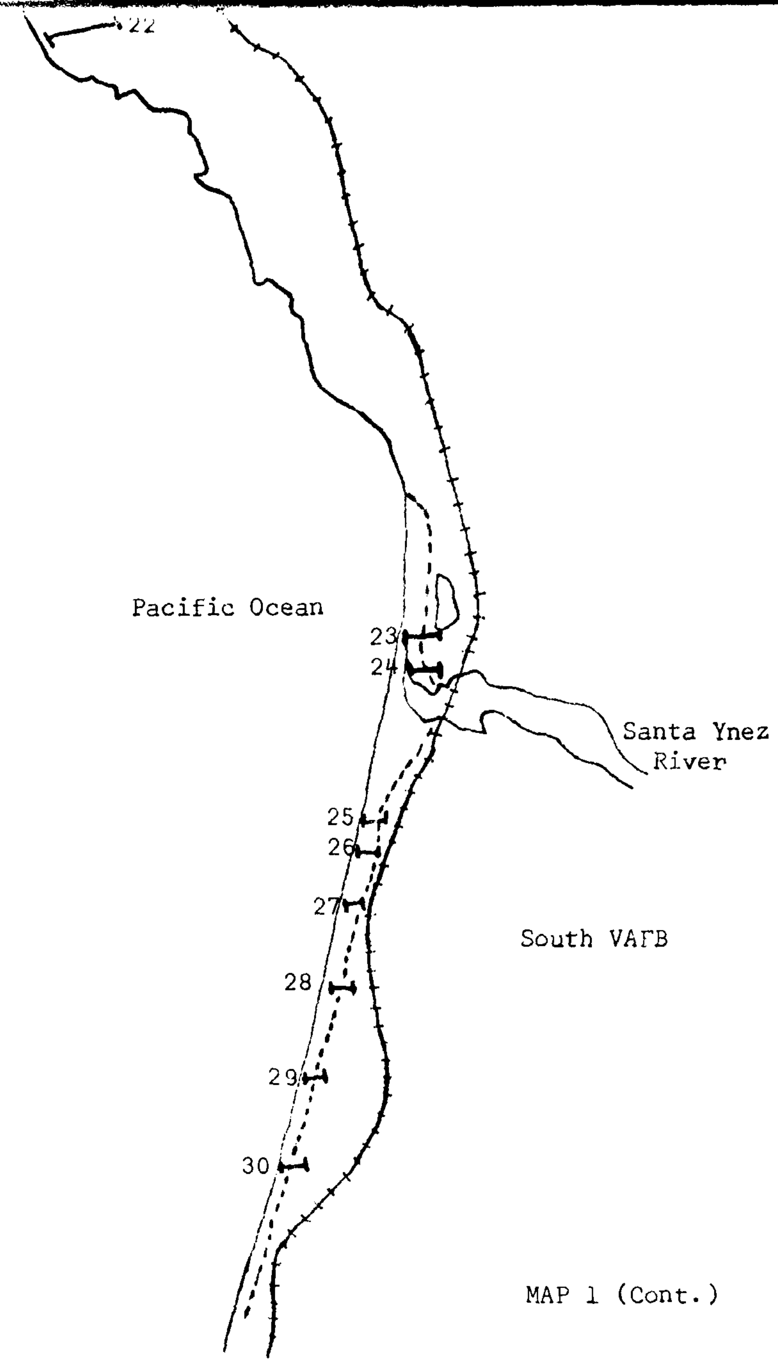
N
Pacific Ocean
San Antonio Creek
North VAFB
Santa Fe Railroad
Purisima Pt.

MAP 1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Pacific Ocean
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Santa Ynez
River
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South VAFB
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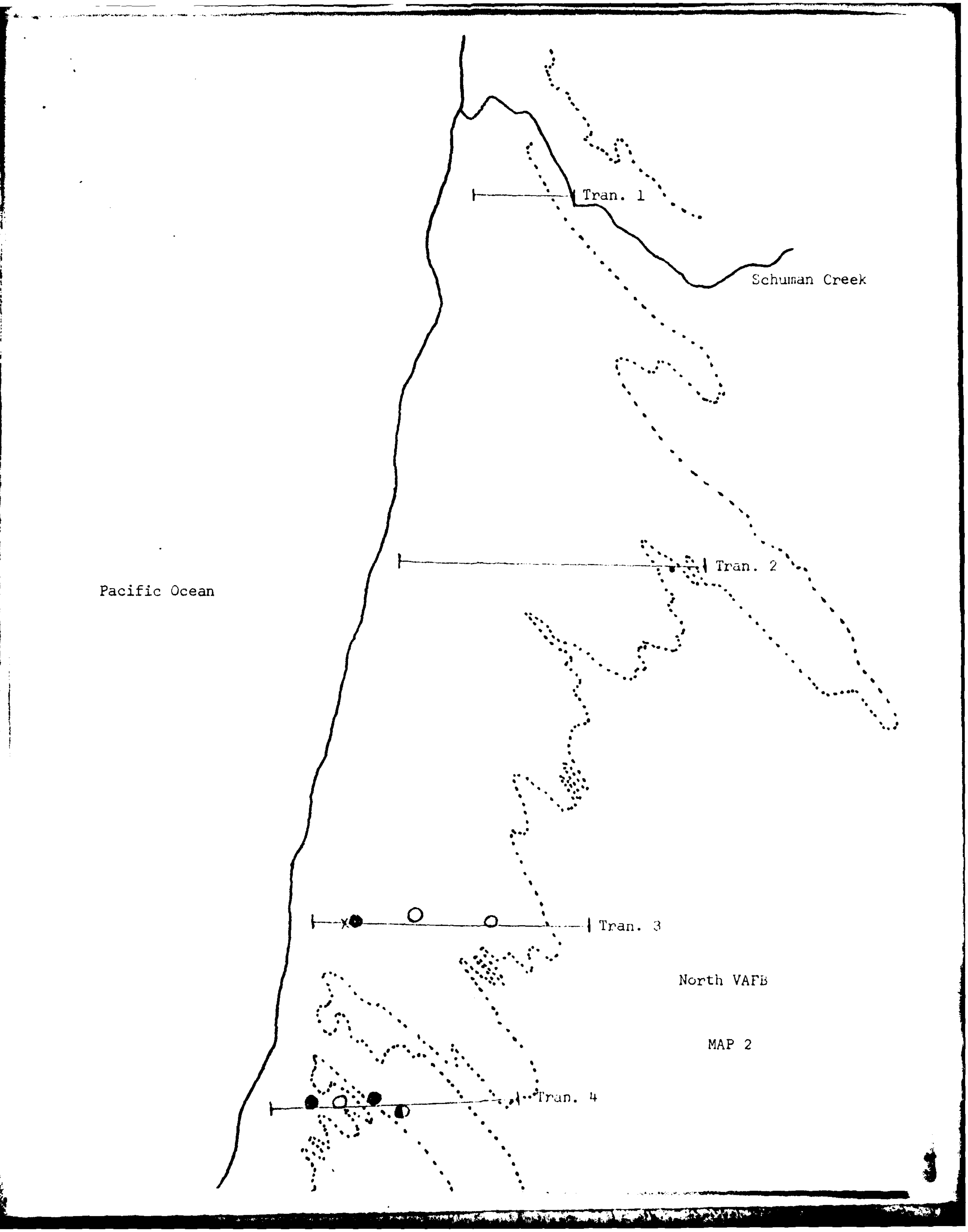
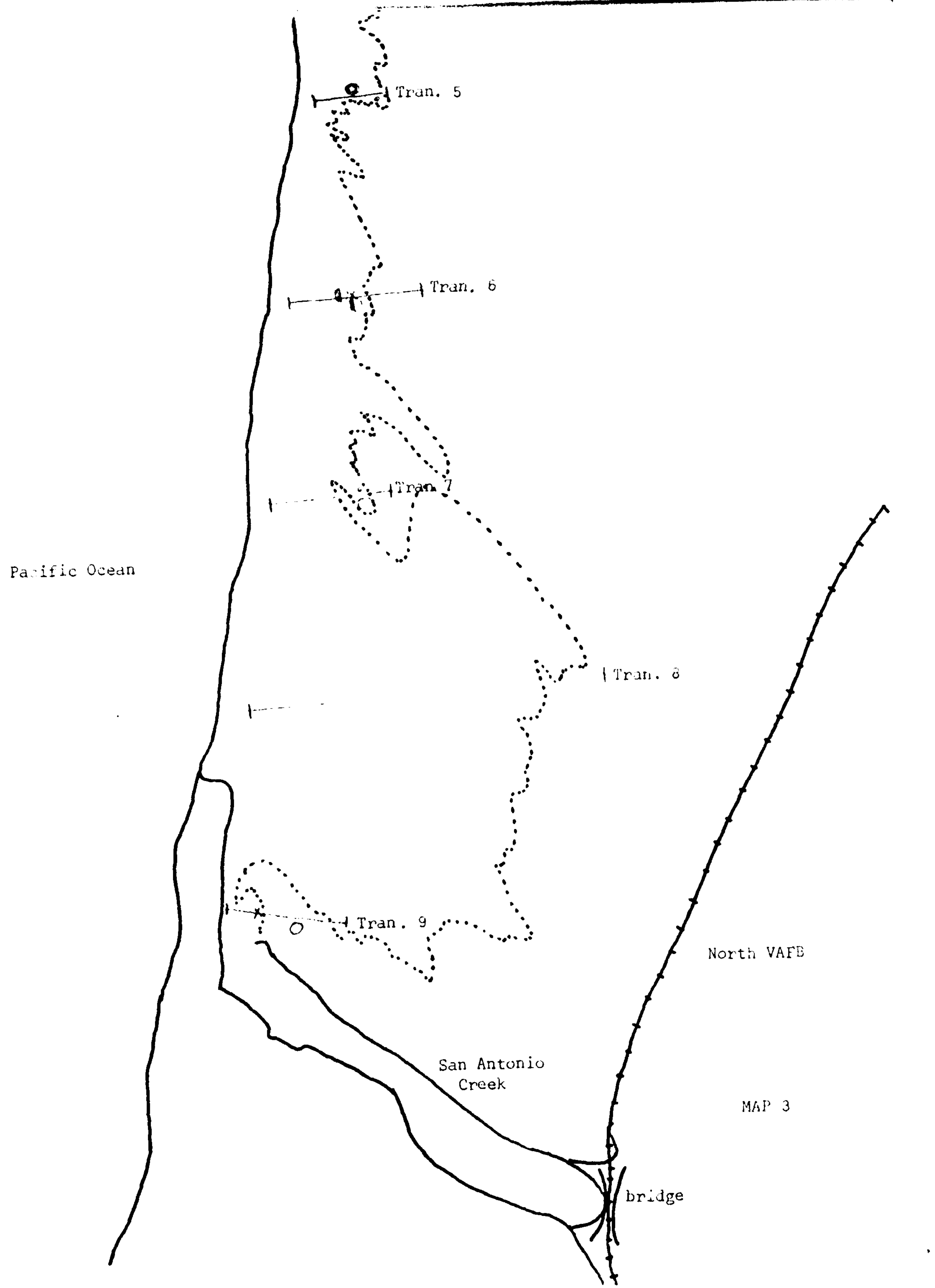
MAP 1 (Cont.)


Tran. 1
Schuman Creek
Tran. 2
Pacific Ocean
Tran. 3
North VAFB
MAP 2
Tran. 4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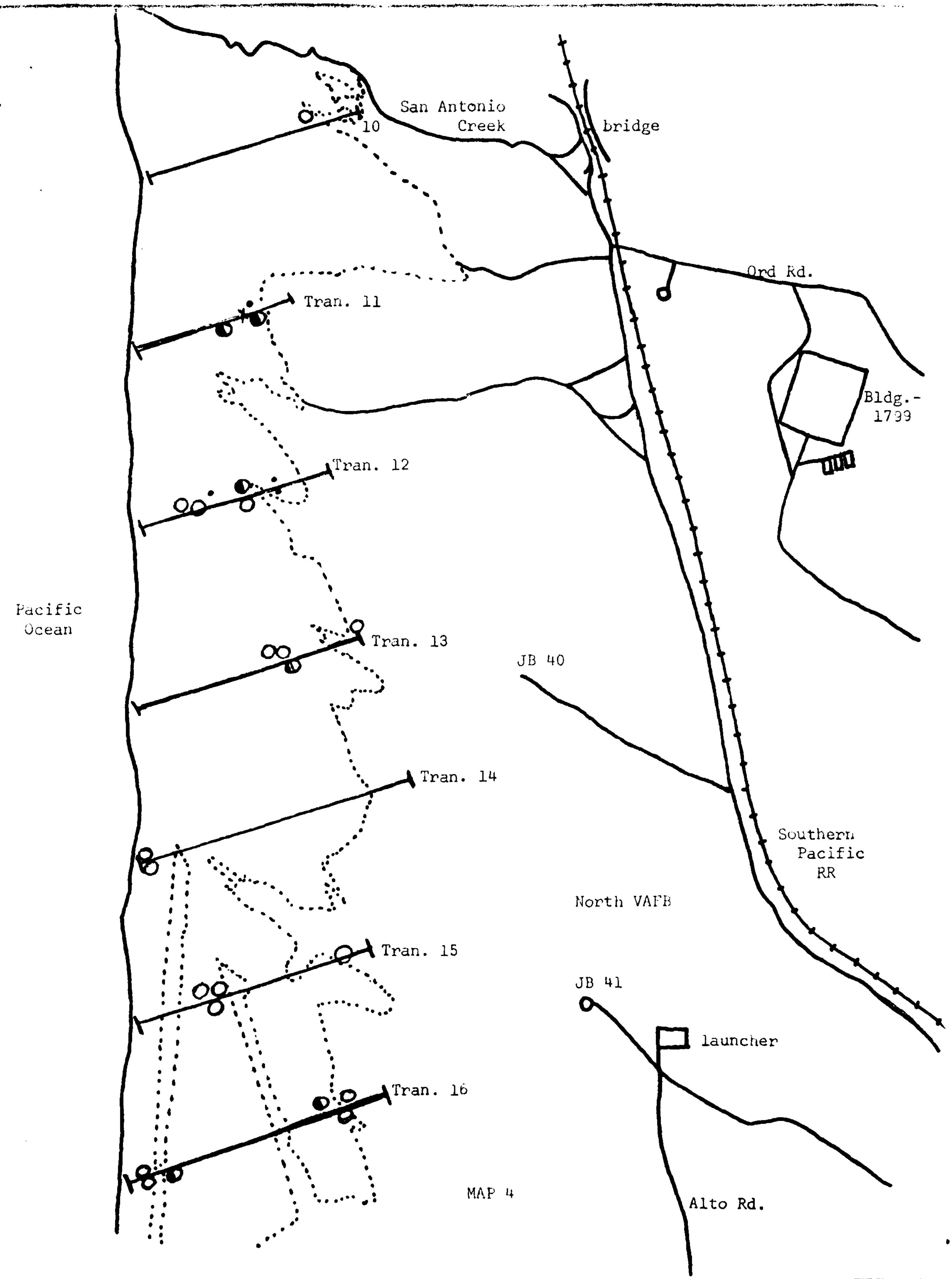
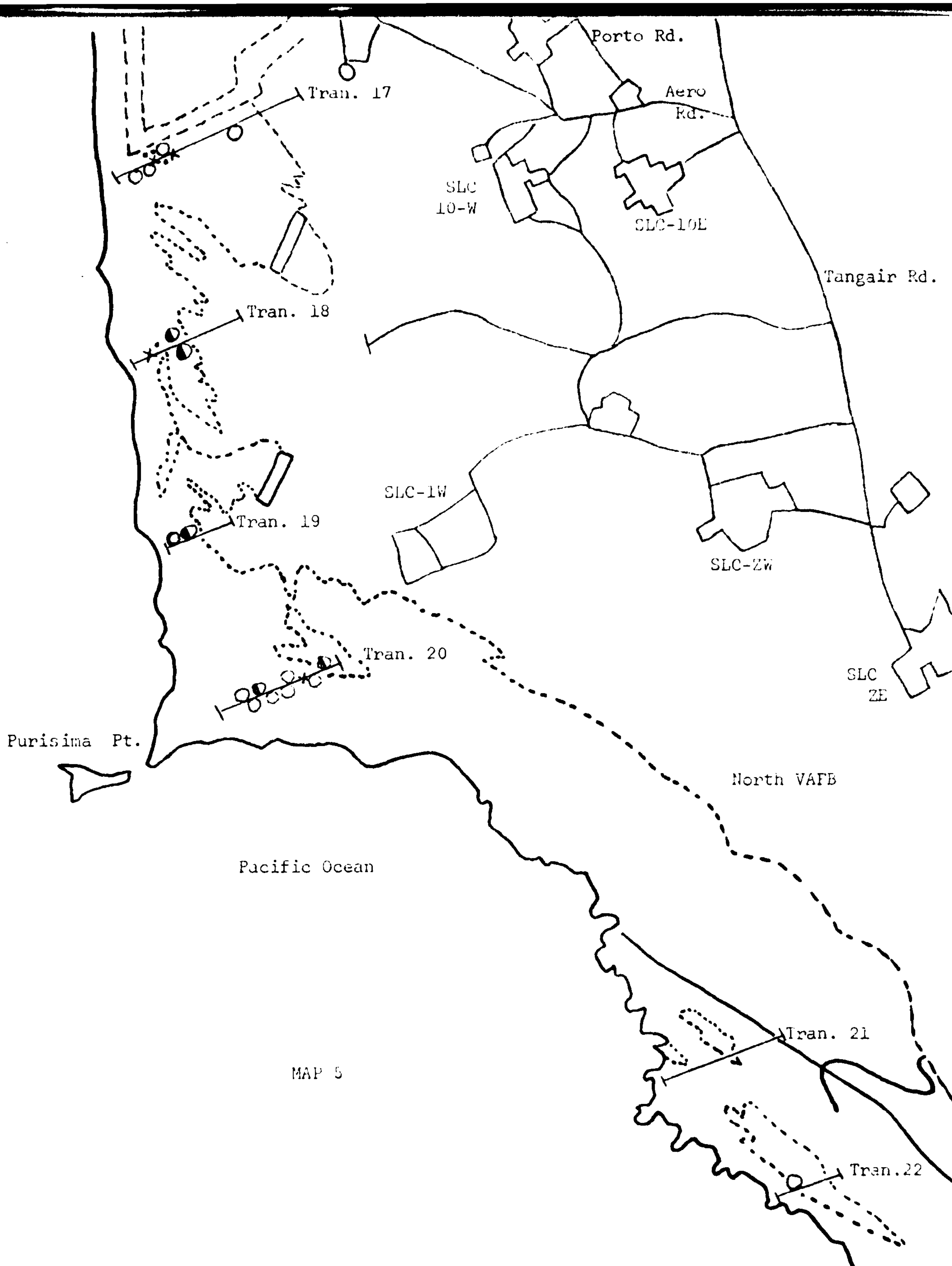
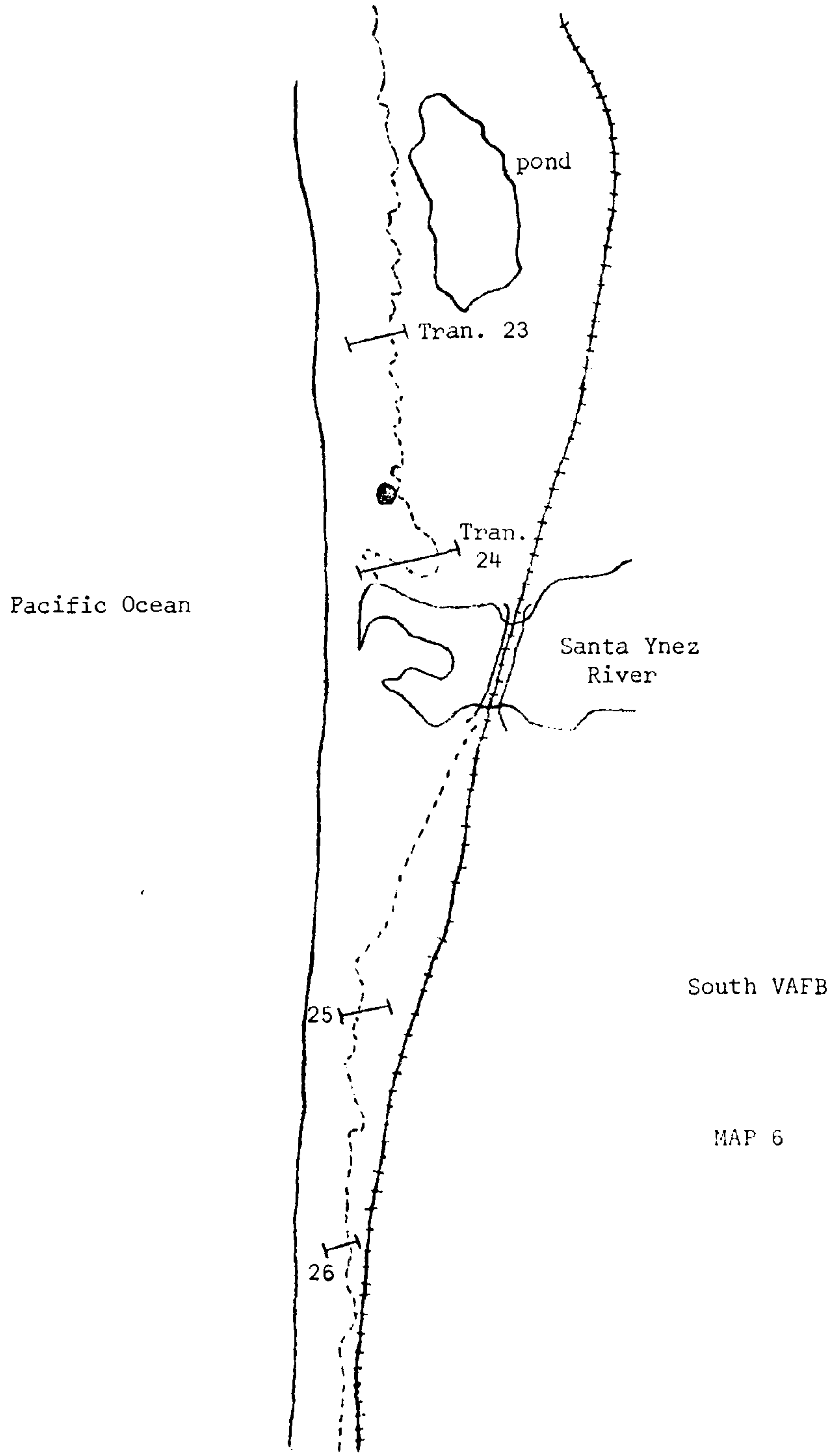
Tran. 6
Tran. 7
Pacific Ocean
Tran. 8
Tran. 9
North VAFB
San Antonio
Creek
MAP 3
bridge

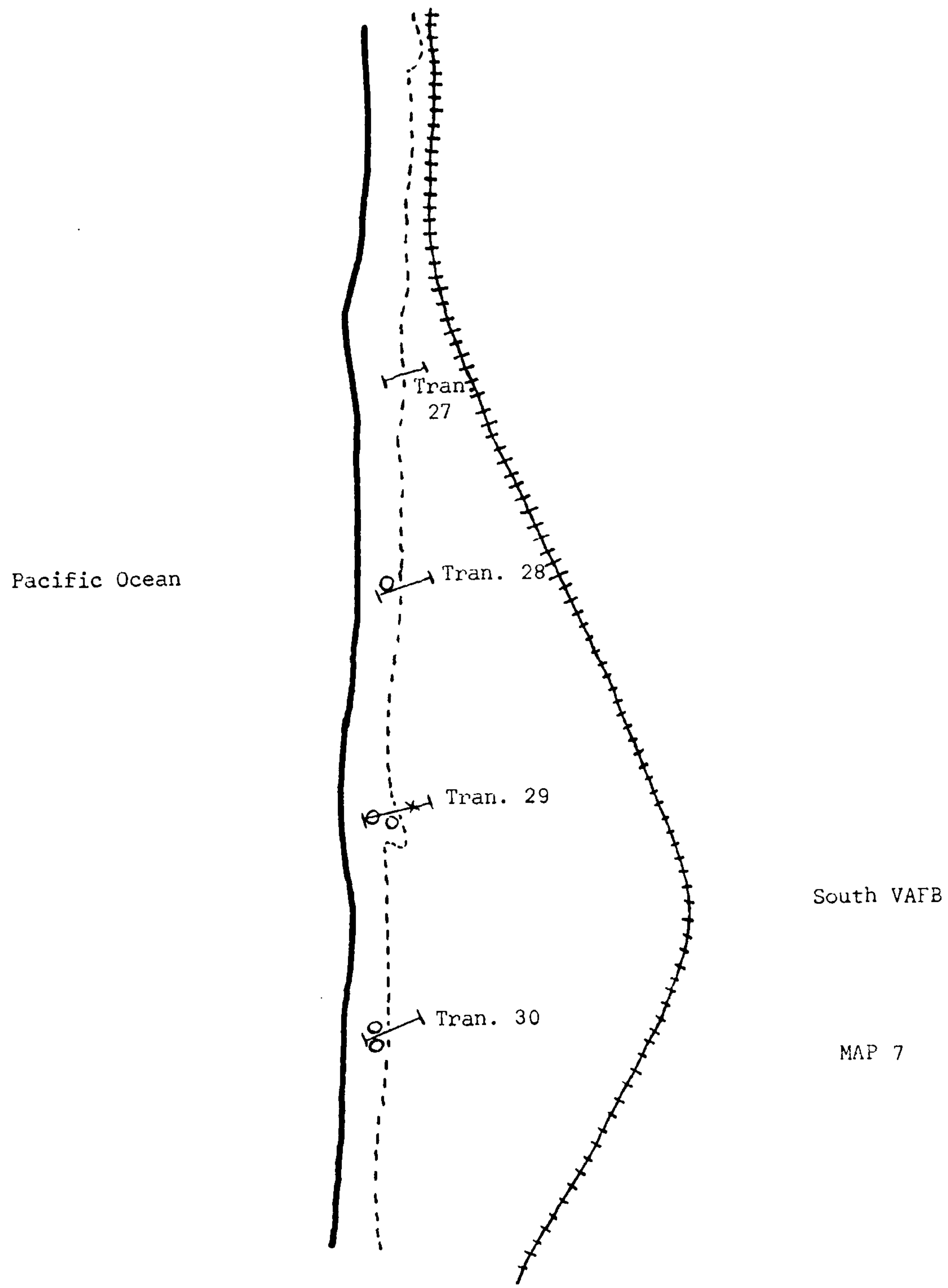

San Antonio Creek
10
bridge
Ord Rd.
Tran. 11
Bldg.-1799
Tran. 12
Pacific Ocean
Tran. 13
JB 40
Tran. 14
Southern Pacific RR
North VAFB
Tran. 15
JB 41
launcher
Tran. 16
Alto Rd.

MAP 4


Porto Rd.
Tran. 17
Aero
Rd.
SLC
10-W
SLC-10E
Tangair Rd.
Tran. 18
SLC-1W
Tran. 19
SLC-2W
Tran. 20
SLC
2E
Purisima Pt.
North VAFB
Pacific Ocean
Tran. 21
Tran.22

MAP 5


pond
Tran. 23
Tran. 24
Pacific Ocean
Santa Ynez River
South VAFB
25
26
MAP 6



MAP 7

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Studies on rare and endangered plant species on the active dunes area of Vandenberg AFB have been completed. The investigation concentrated on the Surf thistle (Cirsium rhothophilum). A detailed examination of the population size and distribution of this species will provide valuable baseline data for evaluating future impacts upon the dunes area of Vandenberg AFB. A rather complete study of the population ecology of C. rhothophilum including seeding, general growth rates, rosette growth and reproduction potential is reported. Recommendations for ecosystem based management of the dunes are also provided.

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